BEHAVIORAL ECOLOGY OF TROPICAL TENT SPIDERS OF THE GENUS *CYRTOPHORA* (ARANEAE: ARANEIDAE)

By

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This work is dedicated to my parents, Samuel and Shulamit Lubin, who shared and encouraged my enthusiasm for biology (and for spiders, too).

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Spiders of the tropical genus *Cyrtophora* exhibit traits which set them apart from other orb-web spiders of the family Araneidae. All *Cyrtophora* species build a non-adhesive web consisting of a fine-meshed horizontal orb-web with irregular barrier webs above and below. The *Cyrtophora* web acts as a knockdown trap, after the fashion of a theridiid space-web or a linyphiid sheetweb. Comparisons of the trapping efficiencies of *C. moluccensis* and *Nephila maculata* proved the web of *C. moluccensis* to be a less efficient trap for flying insects than the typical, adhesive orb-web.

In spite of its relative inefficiency as a trap, the web of *Cyrtophora* species has certain advantages which enable the spider to exploit ecological niches unavailable to other araneid spiders. These advantages include increased web durability and strength, a low frequency of web renewal, and a reduced energetic cost of web maintenance and renewal. By constructing a durable and more-or-less permanent trap, *Cyrtophora* species can exploit exposed habitats in areas that are

regularly [illegible] to heavy rainfall and/or high winds, and can utilize a wide variety of flying insects available during all weather conditions throughout the day and night.

The predatory behavior of four species of *Cyrtophora* was studied and compared with that of other orb-weavers. The prey capture behavior of *Cyrtophora* species was found to be similar to that of *Argiope argentata* and *Eriophora fuliginea*, and included such "advanced" traits as immobilization of prey by wrapping as well as by biting, and transportation of prey on silk dangling from the spinnerets. The similarity between predatory behaviors of *Argiope* and *Cyrtophora* is initially surprising considering the differences in structure and function of their webs. *Cyrtophora* with a non-adhesive, knockdown web and *Argiope* with a typical, adhesive orb-web. Analysis of predatory behavior, web-building behavior, and web structure suggests that *Cyrtophora* evolved from an *Argiope*-like precursor in which "advanced" prey capture behavior was already present. Its web is, therefore, a specialized modification of a typical orb-web. This contrasts with current theories which suggest that *Cyrtophora* is a link between the sheetweb-building Linyphiidae and the Araneidae.

At least two species of *Cyrtophora*, *C. moluccensis* and *C. citricola*, form colonies and exhibit a "communal" level of social organization. *Cyrtophora moluccensis* colony members interact aggressively during prey capture and web repair and renewal. Such interactions may serve as a spacing mechanism ensuring an adequate food supply for each individual *Cyrtophora moluccensis* colonies are conspicuous and persistent. Disadvantages resulting from this include possibly a higher incidence of parasitism in colonies than in solitary orb-web species, and a greater proportion of flying insects that actively avoid the webs. Advantages of communal organization postulated for *C. moluccensis* include increased protection of egg-cases and young, greater prey capture efficiency, greater web building efficiency, and the ability to exploit habitats that are unavailable to solitary species. Evidence is shown for the first and the last of these hypotheses. The degree of protection of young increases from the solitary *C. cylindroides* and *C. cicatrosa* to the most social species, *C. citricola* and *C. moluccensis*.

Cyrtophora moluccensis colonies inhabit open spaces that often bisect major flight paths of insects. Such areas cannot normally be spanned by solitary spiders and, in spite of an abundance of flying insects, they must be considered marginal habitats for web-building spiders. The population dynamics of *C. moluccensis* colonies may fit the pattern of a "fugitive" or colonizing species. Colony growth, in the absence of competition from other araneids, is essentially exponential, and successful colonies of up to 200 individuals were observed. Ballooning was not observed in *C. moluccensis*; however, spiderlings disperse from saturated colonies by climbing through the vegetation. There is good evidence that *C. moluccensis* is carried considerable distances by man, either accidentally, or, in some areas of New Guinea, for ritualistic purposes.

CHAPTER 1. INTRODUCTION

Orb-web spiders (Araneidae) are a conspicuous faunal component of grassland, forest-edge and second-growth rainforest in tropical areas throughout the world. They may be likened to aerial filter-feeders, filtering out and preying on a broad spectrum of flying and jumping insects. Orb-web spiders may be found throughout all levels of vegetation, from herbaceous strata to the forest canopy and thus may be important in regulating population sizes of many groups of flying insects. Considering their diversity and abundance, remarkably little is known about the ecology and behavior of tropical araneids.

Previous studies of the ecology of web-building spiders include those of Kajak (1965a, 1965b, 1967) and Kajak and Olechowicz (1969) on the prey, predatory efficiencies and productivity of *Araneus* species (Araneidae) in temperate grasslands. Turnbull (1960) recorded the prey of the sheet-web spider, *Linyphia triangularis* (Linyphiidae), in a temperate woodland area, and performed laboratory studies on feeding, growth, and assimilation rates of this species (Turnbull, 1962) and of the agelenid, *Agelenopsis potteri* (Turnbull, 1965). Robinson and Robinson (1970) observed the prey of the tropical grassland and forest-clearing araneid, *Argiope argentata*, and the prey of *Nephila maculata* in New Guinea (Robinson and Robinson, unpublished). They have also studied the prey-capture behavior of several tropical araneids, including *Argiope argentata*, *Nephila clavipes* and *Eriophora fuliginea* in Panama, and *Nephila maculata* and several *Argiope* species in New Guinea (Robinson, 1969; Robinson *et al.*, 1969, Robinson and Olazarri, 1971; Robinson and Mirick, 1971; Robinson *et al.*, 1972). The factors involved in web building and web site selection in araneids, important aspects of predatory behavior, were investigated by Witt (1963) and Enders (personal communication).

These studies have shown that web-building spiders in general, and orb-weavers in particular, are opportunistic predators (within certain prey size limitations), and can adapt their feeding habits to fit existing conditions of prey availability. The behavioral studies have also shown, however, that araneids vary considerably in their predatory efficiencies, and that they may utilize different prey-capture strategies with different insect groups. Much remains yet to be learned about the nature of spider-prey interactions and the adaptiveness of predatory behavior

A year's research in New Guinea was planned to study the behavior and ecology of orb-web spiders, for comparison with data on New World tropical and temperate araneids In New Guinea, I was particularly impressed by the diversity and abundance of *Cyrtophora* species (Araneidae) and decided to undertake a comparative study of the more conspicuous members of this genus. I had already noticed some peculiarities typical of this genus in *Cyrtophora citricola* in West Africa and Madagascar, namely, the unusual structure of the orb-web, the tendency to form dense aggregations, and the exposed locations of both the webs and the egg-cases. As the genus is widely distributed throughout the tropical and sub-tropical areas of the Old World, I thought that these, and possibly other adaptations might confer selective advantages under certain conditions. My goal was to analyze some of the behavior patterns typical of species of this genus, and to determine their adaptive advantages and the conditions which might have led to their development. This could be accomplished only by comparing the ecology and behavior of *Cyrtophora* species with those of other orb-weavers.

Further incentive to tackle this problem was provided by the realization that *Cyrtophora*, and a related New World genus, *Mecynogea*, have long puzzled taxonomists who have attempted to determine their affinities to other orb-weavers. As some of the most distinguishing characteristics of *Cyrtophora* species appeared to be behavioral ones, I suspected that a vigorous comparison of behavior patterns between *Cyrtophora* and other araneids would produce clues to the evolution of this genus.

A large part of the results of a year's research on *Cyrtophora* is given here. This includes a study of the function and adaptive significance of the orb-web of *Cyrtophora* (Chapter 2), a comparative study of the predatory behavior of four species of *Cyrtophora* (Chapter 3), and some preliminary research on the adaptive values of colony formation and the population dynamics of *Cyrtophora moluccensis* colonies (Chapter 4). The *Cyrtophora* species studied in detail were *C. citricola* (Forskal) in West Africa and Madagascar and *C. moluccensis* (Doleschall), *C. cylindroides* (Walck.), and *C. monulfi* (Chrysanthus) in New Guinea. Observations were also made on *C. cicatrosa* (Stolicka) and on an unidentified species (sp. "D") in New Guinea. Most of the work was carried out on the grounds of the Wau Ecology Institute and various other locations in the Wau and Bulolo valleys in the Morobe District of the Territory of New Guinea.

The Wau valley is approximately 3000 ft. above sea-level. Its native vegetation has been almost entirely replaced by coffee plantations, small farms and periodically fired "kunai" grassland (dominated by the grasses *Themeda* spp. and *Imperata* spp.; Robbins, 1970). The surrounding slopes, however, are covered mainly by mid-altitude montane rainforest (*Araucaria*-*Nothofagus*-*Castanopsis* associations, Robbins, 1970), "kunai" grassland, and various stages of second-growth forest. *Araucaria* spp. and *Pinus australis* plantations have been established on some slopes.

The average annual rainfall in Wau, based on 10 to 28 year records from three locations in the valley, is 67.60 to 73.19 inches (Brookfield and Hart, 1966), and is distributed relatively evenly throughout the year. The period from October to April is somewhat wetter than average, with 6.8 to 9.3 inches of rain per month (records from Golden Ridges, Wau, Brookfield and Hart, 1966); this period is referred to as the "wet season." The "dry season," from May to September, receives an average of 3.3 to 5.5 inches of rain per month (Golden Ridges). Temperature records are unavailable for Wau; however, we found that during the period of April to May of 1971, daily temperatures varied regularly from a low of 18 to 20°C in the early morning hours to a high of 28 to 30°C around noon.

The Bulolo valley, approximately 2200 ft. above sea-level, is slightly drier than the Wau valley. The average annual rainfall is 60.86 to 64.08 inches (Brookfield and Hart, 1966) and average daily minimum and maximum temperatures recorded at the Bulolo Forestry College during 1969 were 18.9°C and 30.2°C respectively. The Bulolo valley suffered large-scale habitat destruction as a result of gold-mining operations and is covered almost entirely with early stage second-growth vegetation and 'kunai" grassland *Araucaria* plantations and second-growth mid-altitude rainforest are found on the surrounding slopes.

CHAPTER 2 THE ADAPTIVE ADVANTAGES OF THE NON-ADHESIVE ORB-WEB OF *CYRTOPHORA*

Introduction

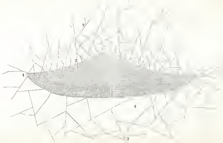
The typical araneid orb-web is composed of both adhesive and non-adhesive elements. The radii, frame threads and structural or temporary spiral are non-adhesive, while the viscid spiral is sticky. The typical orb-web filters out flying insects within a given size range and traps them on the strands of the viscid spiral. Orb-webs vary in such parameters as web size, shape, and strength, mesh (filter) size, orientation and location of the web, and presence of extra-orb constructions, such as barrier webs, retreats and cryptic devices. The variation of orb-web types within the Araneidae has been described by several authors, notably Bristowe (1941), Comstock (1912), Kaston (1964) and Savory (1952).

Spiders of the genera *Cyrtophora* and *Mecynogea* have orb-webs that are both structurally and functionally different from those of other orb-weavers. Kullmann (1958) described the web of *Cyrtophora citricola* from Africa and the Mediterranean. *Cyrtophora moluccensis* in New Guinea builds a similar web (Figure 1), which is composed of the following elements:

1. The orb-web or net, a fine-meshed, horizontal orb. The mesh is so small and regular as to give the appearance of a plankton net. The hub is irregular in shape and continuous with the spiral. The horizontal net is drawn

Figure 1 The 3-dimensional orb-web of *C. moluccensis* (schematic).

1. Orb-web or net
2. Barrier webs
3. Dense snare
4. Thread-free zone


2
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2

upwards at the hub, giving it a domed shape. This is undoubtedly the origin of the name "tent spider" (Main, 1964).

2. The barrier webs: a network of irregular threads above and below the horizontal orb.
3. The dense snare: a layer of short, more-or-less vertical threads connecting the upper surface of the orb-web with the upper barrier web.
4. The thread-free zone: an open zone between the lower surface of the orb and the lower barrier web. Only a few threads, under great tension, connect the orb to the lower barrier web.

The entire web is composed of non-adhesive silk. It is a 3-dimensional structure, as opposed to the typical, 2-dimensional orb-web. Although other orb-weavers construct horizontal webs (e.g., *Tetragnatha* and *Leucauge*) and some construct a barrier web dorsal and/or ventral to a near-vertical orb (e.g., *Nephila* and *Metepeira*), the combination of a fine-meshed, horizontal orb, non-adhesive silk and a complex barrier web is a unique one.

The *Cyrtophora* web functions as a knockdown trap, rather than as a sticky trap (Kullmann, 1958, refers to it as 'Auffangnetz'—a collecting web). Flying insects strike the upper barrier web and drop onto the horizontal net. The spider runs to the prey on the undersurface of the net (in the thread-free zone) and attacks it from below. The net functions as a catching surface and as a platform for the spider. Escape of prey from the surface of the net is difficult due to the fineness of the mesh and the numerous attachments of vertical threads of the dense snare to the upper surface of the net.

Three-dimensional knockdown traps for flying insects occur in other spider families. Flat or domed sheets with barrier webs above them are found among the Linyphiidae, Theridiidae, Agelenidae and Psechridae. The trapping mechanism of these webs is essentially similar, relying on the tendency of flying insects to drop or settle upon encountering an obstacle in flight. Among the large family of orb-weavers, only Cyrtophora (Old World) and Mecynogea (New World) have evolved a knockdown trap.

It has been suggested (Kaston, 1964, Kullmann, 1958) that the knockdown web of Cyrtophora preceded the evolution of the typical araneid orb-web, and may, in fact, be a link between a linyphiid-type sheetweb and a Nephila-type adhesive orb-web. For reasons which will be discussed later, I think it more likely that the knockdown webs of Cyrtophora and Mecynogea evolved from a typical orb-web through loss of the viscid spiral and evolution of a 3-dimensional barrier web. If this is the case, what are the advantages of the knockdown web in comparison with the typical, adhesive orb-web? Two possibilities are suggested.

1. The knockdown web is a more efficient trap than the sticky orb-web.
2. The knockdown web is stronger and more durable than the typical orb-web, and is energetically advantageous under conditions where frequent damage to the web is likely to occur.

With these hypotheses in mind, experiments and observations were conducted on knockdown webs of *C. moluccensis* and on sticky webs of *Nephila maculata* (Fabricius) and *N. clavipes* (L.), comparing their trapping efficiencies, the strength of various web elements, and web durability. The energy content of *Nephila* and *Cyrtophora* webs was measured and estimates made of the energetic cost of web-building.

Materials and Methods

Cyrtophora moluccensis occurs throughout New Guinea, particularly in the vicinity of human habitation. It is generally found in colonies of up to 200 individuals. The individual webs in a colony are interconnected, so that the upper barrier web of one spider is continuous with the lower barrier web of the spider above it. Colonies occur in open habitats: in pine and araucaria trees, in citrus plantations, and along telephone wires and fences. Solitary *C. moluccensis*, or small aggregations, may be found in tall grass and shrubs along the roadside, and in small ornamental trees. All experiments and observations were conducted on webs of adult *C. moluccensis*. The majority of the work was carried out at the Wau Ecology Institute in Wau, Territory of New Guinea.

Nephila maculata, the giant wood spider, occurs in forest understory, along forest edges, and in clearings in New Guinea. It constructs a vertical, relatively close-meshed, sticky web, of slightly larger diameter than the orb-web of *C. moluccensis*. Although *N. maculata* is a larger spider than *C. moluccensis*, it is convenient for comparison, since it is the only large orb-weaver with a fine mesh, sticky web to occur in relatively open areas. *Nephila maculata* sometimes places its web on the periphery of C. moluccensis colonies. Characteristics of these two species and their webs are summarized in Table 1.

Capture Efficiencies

Capture efficiency of a web is defined here as success in trapping and restraining prey in the spider's absence. This is different from the overall prey capture efficiency, which takes into account both the trapping and restraining efficiency of the web and the prey capture behavior of the spider. In comparing the efficiency of the knockdown web of C. moluccensis and that of the adhesive web of N. maculata, these two components were evaluated separately.

Capture efficiencies of webs were determined in the following manner: ten blowflies each were flown into webs of C. moluccensis and N. maculata from which the spiders had been removed. The number of flies initially caught by the web (trapping efficiency) and the amount of time they remained trapped in the web (restraining efficiency) were determined.

Overall prey capture efficiencies were determined by flying blowflies into occupied webs of C. moluccensis and N. maculata at 1-minute intervals, and recording the number of flies caught by the spiders and the speed of response to blowflies in the web. The time elapsed until initiation of an attack on the prey is used as a measure of the speed of response of the spider.

Only isolated (solitary) webs of C. moluccensis were used in these experiments, in order to avoid interactions between spiders of adjacent webs that would occur in a colony. The blowflies were held in a plastic bag and released singly 2 ft. from the web under observation.

Table 1. Comparison of C. moluccensis and N. maculata body size, web and habitat characteristics.

	C. moluccensis	N. maculata
Length (mm)	♀: 20-28 (Chrysanthus, 1959) ♂ 4-5 (Chrysanthus, 1959)	♀: 32-42 (Chrysanthus, 1959)
Weight (g)	♀: 0.58-1.99 $\overline{x}$ = 1.163 n = 27	♀: 2-4 (Robinson, pers. comm.)
Habitat	Open areas: pine and araucaria trees, fences, telephone wires	Forest understory, clearings, forest edge
Gregariousness	Colony forming, rarely solitary	Solitary
Web Orientation	Horizontal	Vertical or near vertical
Diameter of Orb (cm)	max: 38-81 $\overline{x}$ = 64.2 min: 36-81 $\overline{x}$ = 59.2 n = 10	width: 62-100 $\overline{x}$ = 84.1 length: 79-116 $\overline{x}$ = 96.2 n = 10 (Robinson and Robinson, unpublished)
Mesh Size (mm)	3-5	variable (approx. 10)
Barrier Web	Upper and lower barrier webs always present[1]	Sometimes present on one or two sides[1]
Viscid Spiral	Absent	Present
Structural Spiral	Present, evenly spaced	Present, but unevenly spaced

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[1] The barrier webs of *Cyrtophora* and *Nephila* are probably of different evolutionary origins.

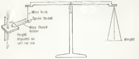
Only those actually striking the web were recorded. Blowflies were used for these experiments because they tend to fly in a straight line when released and are within the normal size range of prey of both *C. moluccensis* and *N. maculata*.

Web Durability and Strength

Field studies were conducted on the frequency and extent of web renewal in *C. moluccensis*. Forty-one webs were marked and examined daily for 3 1/2 months for signs of renewal. New orb-webs could be readily distinguished from old ones by their color and mesh regularity. Four webs were sprayed with non-toxic yellow paint (spider temporarily removed) and the extent and type of daily repairs noted over a period of one week. Since the web is non-adhesive, the spray paint did not impair its ability to trap prey. The behavior of the four spiders appeared normal in all respects.

Relative tensile strength of web fibers was measured with the apparatus shown in Figure 2. A simple chemical balance was used, with pans and holders replaced by a small weighing pan on one side and a fine copper hook on the other. Sections of web, cut out with the lighted end of a cigarette, were attached to a wire frame or thread holder with fast-drying household glue. The thread holder was similar in design to the one used by Eisner *et al.* (1964) in their studies on the adhesiveness of the viscid spiral of *Nephila clavipes*. The distance between the prongs of the holder was 5 mm, the maximum mesh size of a *C. moluccensis* web. The thread holder could be moved freely along a vertical rod. Thread strength was measured by placing the hook under it and adding weights to the pan until the thread broke.

Figure 2 Apparatus for measuring the relative tensile strength of spider webs.


Wire hook
Spider thread
Wire thread holder
Height adjusted on vertical rod
Weight

Ten measurements were taken from each web. As the entire apparatus was made and used under field conditions, accurate weights below 50 mg were unavailable. Two sizes of lead shot, weighing approximately 11.4 mg and 30.5 mg were used in lieu of small weights.

Tensile strength is generally expressed as the breaking force per unit area, with the force acting parallel to the line of extension. Due to the above method of measurement and to the extensibility of silk fibers, the force measured in these experiments is not the actual breaking force, but is proportional to it. The breaking forces thus measured can only be compared on a relative basis. However, recent tests on tensile strength of threads from *N. clavipes* webs, in which a force was applied parallel to the axis of extension, resulted in breaking forces of similar magnitude to those measured by the above method.

Determinations of breaking force were made on the viscid spirals of *N. maculata*, *Argiope picta* and *A. aemula* webs, on the non-adhesive spiral of *C. moluccensis* webs, and on the structural spiral of *N. maculata* webs. Web samples of *C. moluccensis* and *N. maculata* were kept for 2 to 3 weeks in screened enclosures that were shielded from the rain, but otherwise subject to natural temperature and humidity regimes. The breaking force was measured after 24, 48 and 72 hours, and after 1, 2 and 3 weeks, in order to detect possible changes in web strength with time.

Cost of Web Construction

The total energetic cost of web-building in a spider includes two sources of energy expenditure: energy contained within the silk and energy expended during building activities. This is described in the following equation:

Total cost of web (cal.) = energy content of web (cal.) + active metabolic rate (cal./hr.) X web-building time (hr.).

The costs of web-building and web-renewal for *C. moluccensis* are compared with the cost of web-building for *N. clavipes*. As data on web energy content were unavailable for *N. maculata* from New Guinea, *N. clavipes* from Florida was used instead. *Nephila clavipes* is comparable to *C. moluccensis* both in body weight and diameter of the orb-web (see Table 6).

The energy content of a web was determined by direct calorimetry. Webs of *C. moluccensis* from Wau, New Guinea, and *N. clavipes* from Gainesville, Florida, were dried to a constant weight and combusted in a Parr Adiabatic Oxygen-Bomb Calorimeter. Corrections for nitric acid and unburned fuse wire were determined for each sample. The methods used are described in the Parr Instrument Co. Manual No. 130.

True active and resting metabolic rates are unknown for orb-web spiders. Methods have not yet been devised to measure resting metabolism of a spider sitting on its web, or the metabolic rate of a spider constructing a web. Rough estimates of resting metabolism can be made using conventional respirometry (e.g., a Warburg apparatus or differential respirometer). Measurements of O_2—consumption of *C. moluccensis* and *N. clavipes* give an estimate which may be termed an average metabolic rate. This is an average of the O_2 uptake of spiders sitting still and moving around in a respirometry flask. The methods used to determine average metabolic rates of *C. moluccensis* and *N. clavipes* are described in Appendix 1.

Approximate web-building durations are known for *C. moluccensis* and *N. clavipes*. As the metabolic rate and web-building duration are both approximations, the possible error in the value of their product may be quite large. The amount of energy expended during web-building is small in comparison with the energy content of the web itself and may be ignored in a final computation of the total cost of the web. Thus, the cost of web-building is reduced essentially to the energetic cost of the silk itself.

Results and Discussion

Capture Efficiencies

Trapping and restraining efficiencies of unoccupied *N. maculata* and *C. moluccensis* webs are shown in Table 2. The majority of escapes from *Cyrtophora* webs are due to blowflies flying straight through the web. This accounted for 55 percent of the escapes from *Cyrtophora* webs, and only 14 percent of the escapes from *Nephila* webs. Thus, the initial trapping efficiency of the knockdown web is lower than that of the sticky web. Furthermore, only 16 percent of the blowflies were restrained for more than 1 minute by unoccupied *Cyrtophora* webs (omitting 6 percent caught by theridiid web parasites), while 70 percent were restrained by *Nephila* webs (omitting one theridiid capture). The non-adhesive *Cyrtophora* web is clearly less effective in both trapping blowflies and preventing their escape than the sticky *Nephila* web.

It was found that blowflies trapped in unoccupied *Cyrtophora* webs for more than 1 minute were invariably trapped on the horizontal net. Small, compact insects, such as blowflies, can readily fly straight

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Table 2. Trapping and restraining efficiencies of unoccupied *C. moluccensis* and *M. maculata* webs: percentages of blowflies trapped and held by the webs.

Time Held by Web (min.)	*C. moluccensis* n = 100	*M. maculata* n = 100
straight through web	55	16
< 1'00	23	13
1'00 – 4'59	9	24
5'00 – 9'59	1 + 1 inq. capt.[1]	8
> 10'00	6 + 5 inq. capt.	38 + 1 inq. capt.

---

[1] Blowflies captured by theridiid inquilines (web parasites).

through the barrier web; however, once they fall onto the net, escape becomes more difficult. An analysis of motion pictures of prey capture sequences in *Cyrtophora* spp. shows that insects' tarsi are repeatedly caught in the fine mesh as they attempt to walk on the net. The dense zone of vertical threads immediately above the net further impedes movement.

The mean speed of response or time it takes for a spider to seize a blowfly caught in the web, was less than 10 seconds for both *Cyrtophora* and *Nephila* (Table 3), and was not significantly different for the two species. Thus, any difference between *Nephila* and *Cyrtophora* in the proportion of captures must be due to the different trapping and restraining efficiencies of their webs.

Overall capture efficiencies of *C. moluccensis* and *N. maculata* with blowflies presented at 1 minute intervals are compared in Figure 3. Even with the spider present, there were more escapes from *Cyrtophora* webs. The majority of escapes from occupied *Nephila* webs were due to blowflies flying straight through the webs, undetected by the spider. Nearly all flies actually trapped in the sticky web were caught by the spider. This was not the case with *Cyrtophora*, where a large proportion of blowflies escaped after being initially restrained by the web.

The relative inefficiency of *Cyrtophora*, as just described, may be partly compensated for in later stages of the prey capture sequence. The stages during which losses may occur are listed below, together with the type of efficiency concerned:

1. Losses through the web (trapping efficiency of the web).

Table 3 Speed of response of C. moluccensis and N. maculata to blowflies flown into webs at 1-minute intervals. Only actual captures are considered.

	n	Mean Speed of Response	S.D.
C. moluccensis	38	8.7 sec.	13.2
N. maculata	73	6.9 sec.	9.0

(t = 0.97)

2. Pre attack losses in the web (restraining efficiency of the web and speed of response of the spider)
3. Losses during prey capture (prey capture efficiency of the spider).
4. Losses to web parasites (prey storage efficiency of the spider)

Losses during immobilization of prey, transport to the hub or losses at the hub itself may be reduced in *Cyrtophora*, at least with certain prey types. *Cyrtophora*, like *Argiope*, can immobilize prey from a distance by wrapping in silk (see Chapter 3). Thus, large prey may be restrained more rapidly, and a variety of dangerous insects and insects with noxious secretions may be safely attacked. Immobilization of prey by wrapping may selectively reduce losses of such prey types as hymenopterans, pentatomids and large beetles. By shortening the duration of prey capture, immobilization wrapping may also minimize pre-attack losses in the web and losses to web parasites.

Robinson *et al.* (1969) computed the overall prey capture efficiencies of *Nephila clavipes* and *Argiope argentata* using stingless bees presented at 30-second intervals. They found that while *Argiope* lost more prey due to insects flying straight through the web (lower trapping efficiency of the web), *Nephila* incurred more losses at later stages of the prey capture sequence (lower prey capture efficiency of the spider). The overall prey capture efficiency of *Nephila* was lower than that of *Argiope*. This is mainly due to the predatory behavior of *Argiope*, whereby wrapped prey are left at the capture site while a new predatory sequence is initiated.

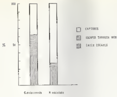
The elimination of one stage of prey capture (transport of prey to the hub) enables *Argiope* to attack insects presented in rapid succession with greater speed and efficiency. Unlike *Argiope*, *Cyrtophora* does not leave wrapped prey in the web (see Chapter 3) and, therefore, has an advantage over *Nephila* in dealing with small prey presented in rapid succession.

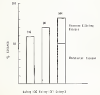
Insects striking the web in rapid succession, or 1-minute intervals, may represent a rather unrealistic situation. As a check on the above results, insect escapes were recorded by direct observation from two natural colonies of *C. moluccensis* (Figure 4). Escape amounted to 58 to 80 percent of the insects actually striking the colony. Although their data are not strictly comparable, Robinson and Robinson (1970) recorded only 5 percent escapes from single webs of *Argiope argentata* in Panama. These were determined by the number of holes in webs which could not be accounted for by prey actually found in the web. The resulting figure is certainly low, as some small insects can fly straight through the wide-meshed web of *Argiope* without leaving holes. Nonetheless, the proportion of escapes from *C. moluccensis* colonies may approach 10 times that of escapes from *Argiope* webs.

Escapes from colony 3 (Figure 4) were separated into insects that elicited prey capture responses (e.g., plucking or tensioning of the web, or running toward the prey) in at least one spider and insects that escaped without eliciting prey capture responses. Based on these observations, over 30 percent of the insects striking the colony escaped in spite of having been detected by one or more spiders. These response-eliciting escapes are the costly ones, in terms of

Figure 3. Overall prey capture efficiencies of *C. moluccensis* and *N. maculata*: percentage of blowflies caught and percentage escapes from webs. Blowflies presented at 1 minute intervals (n = 100)

Figure 4. Insect escapes from two *C. moluccensis* colonies, based on 85 hours of direct observation. Number above bar indicates total number of insects observed striking the colony.


100
%
50
CAPTURES
ESCAPES THROUGH WEB
LATER ESCAPES
C.malaccensis
N maculata


100
50
% ESCAPES
397
161
574
Response Eliciting Escapes
Undetected Escapes
Colony 1(a)
Colony 1(b)
Colony 3

energy wasted by the spider in unsuccessful prey capture attempts. The ratio of successful captures to prey capture responses—the capture index—was calculated for *C. moluccensis* and *N. maculata* with blowflies presented at 1 minute intervals (Table 4). This ratio is higher in *Nephila*, again showing that thr overall prey capture efficiency of *Cyrtophora* is less than that of *Nephila*.

In summary, the knockdown web of *C. moluccensis* is less successful in both trapping and restraining blowflies than the adhesive web of *N. maculata*. Although this may not apply equally to all types of flying insects, data on the large proportion of escapes from natural colonies of *C. moluccensis* support the contention that the knockdown web is, on the whole, a less efficient trap.

Web Durability and Strength

Web renewal in *Cyrtophora* is infrequent and normally only a small portion is renewed. Marked webs of *C. moluccensis* were renewed once every 2 1/2 weeks on the average. The frequency of web renewal in this species, based on a 3 1/2 month census, is given below.

No. Webs	Mean No. Days Between New Webs	S.D.	S.E.M.	Range
41	17.9	12.25	1.94	2-51

During web renewal the horizontal net and part of the dense, vertical snare are cut out (working from the periphery toward the hub), rolled into a ball, and discarded by the spider. The upper and lower barrier webs are not rebuilt, unless they have been accidentally removed or destroyed. The discarded portion of the old web amounted to only about 11 percent of the total web by weight (Table 6).

Table 4. Capture indices of *C. moluccensis* and *N. maculata* (successful attempts divided by total capture attempts). Blowflies presented at 1 minute intervals

	n	No. Prey Capture Attempts	No. Caught	Capture Index
C. moluccensis	100	69	38	.551
N. maculata	100	78	73	.936

Daily repairs in *C. moluccensis* are also limited. In webs sprayed with yellow paint, repairs were confined to the spinning of a network of threads over holes in the horizontal net. These holes, which were mainly the result of prey capture activities, amounted to less than 1 percent of the area of the orb per day. Holes less than 1 cm in diameter were often not repaired for several days. The method of web repair has been described by Kullmann (1958) for *C. citricola*. No major repairs could be detected in the barrier webs, though the addition of some strengthening threads may have gone unnoticed. During observations of *C. moluccensis* colonies at night (all web repairs and web renewal occur at night), individuals were seen climbing through the barrier webs. They appeared to be testing thread attachments and laying down strengthening threads. The extent of these daily repairs, whether on the net or in the barrier webs, is probably negligible in comparison with the total amount of silk in the web.

The pattern of web renewal and repair in *Cyrtophora* is markedly different from that of other orb-weavers. Most araneids renew their entire webs daily and ingest the old web rather than discard it. *Argiope argentata* in Panama generally renews its viscid spiral every morning (Robinson and Olazarri, 1971). *Gasteracantha* species tear their webs down at night, leaving only a few frame threads. *Nephila maculata* in New Guinea was found to rebuild 1/4 to 3/4 of its web daily (Robinson and Robinson, unpublished) and *N. clavipes* in Gainesville, Florida, renews approximately 1/3 to 1/2 of its web each morning. In *Nephila* an entire segment of the web is renewed, including the radii, structural spiral, and viscid spiral.

The cues that trigger destruction of the old web and new web construction in araneids are poorly known. Araneids which renew their webs daily may follow a circadian rhythm. Witt *et al.* (1968) found that temperature, humidity, light regimes, starvation and presence of prey could all influence web-building frequency in caged orb-weavers. Web renewal in *C. moluccensis* is irregular in frequency, even within a single individual, and may depend more on the degree of web damage than on environmental periodicity.

The unusual pattern of web renewal in *Cyrtophora* suggests that *Cyrtophora* web silk is different from that of other araneids. Tests of thread strength of new webs (Table 5 and Figure 5) showed that the non-sticky spiral of a *C. moluccensis* web has approximately 4 times the strength of a *N. maculata* viscid spiral, 6 times that of an *Argiope aemula* viscid spiral and 15 times that of an *A. picta* viscid spiral. Kullmann (1958) examined sections of *C. citricola* webs microscopically and could detect no differences between spiral and radial threads of the orb-web. Thus, the *Cyrtophora* web appears to be constructed entirely of strong, structural threads. My own observations of *Cyrtophora* web-building verify this conclusion. The specific glandular origin of *Cyrtophora* web silk is not known. The structural spiral of *N. maculata* is even stronger than that of *C. moluccensis*. Unlike other orb-weavers which ingest the structural spiral while constructing the viscid spiral, *Nephila* species retain the structural spiral in the completed web. This added strengthening may account for the fact that *Nephila* renews only part of its web daily.

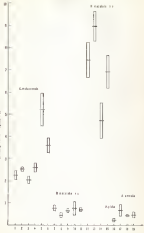
Table 5. Breaking force of new webs, in dynes x 10^3
(10 tests on each web).

S.D. = standard deviation

	No. of Webs	Mean ± S.D.	Range of Means
C. moluccensis spiral	6	3.048 ± 1.189	2.069 - 5.220
N. maculata viscid spiral	5	.678 ± .134	.459 - .798
N. maculata structural spiral	4	7.002 ± 1.750	4.713 - 8.936
Argiope picta viscid spiral	1	.237	---
A. aemula viscid spiral	3	.539 ± .136	.431 - .691

Figure 5. Breaking force of new webs of *C. moluccensis*, *N. maculata*, *A. picta*, and *A. aemula* (in dynes $\times 10^3$). Horizontal lines are means of 10 measurements, bars represent 1 standard deviation.

1-6	*C. moluccensis* spiral
7-11	*N. maculata* viscid spiral
12-15	*N. maculata* structural spiral
16	*A. picta* viscid spiral
17-19	*A. aemula* viscid spiral


M macalata s s
C.malaccensis
Breaking Force dynes x 10^3
10
9
8
7
6
5
4
3
2
1
M macalata v s
A armata
A.picta
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

Thread strength does not deteriorate significantly with time. Webs of *Cyrtophora* and *Nephila*, tested over a period of 3 weeks, showed no marked decline in breaking force (Figure 6).

Lack of a viscid spiral and greater overall thread strength contribute to the durability of the *Cyrtophora* web. In general, damage to orb-webs may occur during prey capture, or as a result of heavy rains or wind. In each case, the *Cyrtophora* web has advantages over the typical orb-web.

Web damage during prey capture

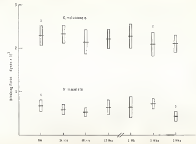
The viscid spiral of a typical orb-web is frequently damaged by prey. An insect that becomes stuck to an adhesive strand struggles to escape. Due to their weakness, several strands of the spiral may be broken at this time. Even when the threads remain intact, that particular portion of the web is virtually useless for further prey capture, as the viscid droplets are worn off. In many species, a large portion of the web is destroyed during removal of the prey from the capture site and transport to the hub.

Since the spiral of a *Cyrtophora* web is both strong and non-sticky, little damage occurs during prey capture. As the radii and spiral of a *Cyrtophora* web are composed of the same type of silk, the net as a whole is a relatively strong structure. Normally, the damage to a *Cyrtophora* web during prey capture is confined to a small hole cut in the horizontal net, through which the spider pulls its prey down to be wrapped.

Web damage from rain or wind

Sticky orb-webs are either partly or wholly taken down and ingested during heavy rains. Even in the case of *Nephila* webs,

Figure 6. Breaking force of aged webs of _C. moluccensis_ and _N. maculata_ (in dynes x 10^3). Horizontal lines are means of 10 measurements, bars represent 1 standard deviation.


3
2
1
Breaking Force dynes x 10^3
C. moluccensis
N maculata
3
2
4
3
NW
24 Hrs
48 Hrs
72 Hrs
1 Wk
2 Wks
3 Wks

which retain the strong structural spiral, large sections are removed by the spider, especially from areas below the hub. It appears that the spider ingests the web rather than lose energy through web destruction by rain.

Langer (1969) derived equations describing the effects of gravity-loading of dew or raindrops on web elements. He did not, however, deal with the case of continuous rapid-loading on web elements which must occur during heavy rainfall. Several factors may be important in determining the effect of rainfall on webs.

a. The number of droplets hitting a web element per unit time, or rate of loading.

b. The force of the droplets hitting the thread.

c. The weight of the droplets that remain sticking to the thread.

The response of a web, too, may depend on several characteristics:

a. Maximum stress tolerated by web elements.

b. Elastic extensibility of the threads.

c. Number and distribution of connections between threads.

d. Web orientation.

e. Nature of web attachments to supports.

f. Wettability and absorbency of thread surface.

The advantages of the *Cyrtophora* web over the sticky orb-web are apparent: 1) the maximum stress tolerated by *Cyrtophora* web elements is greater (larger breaking force), 2) due to the fine mesh (i.e., many thread connections) of uniform size and thread type, the forces would be distributed evenly over the net, 3) due to its 3-dimensional mature and large number of radii, the *Cyrtophora* web has many more connections to its supports than the sticky web.

The disadvantages of the viscid spiral of a sticky orb-web during rain are not immediately clear. The viscid spiral is considerably more elastic than the non-sticky spiral threads of a *Cyrtophora* web. Theoretically, a thread with greater elasticity should withstand greater stress than a non-elastic thread of the same diameter. However, in the case of the viscid spiral, increased elasticity is concomitant with smaller thread diameter, and therefore, less tensile strength. It is also possible that rain reduces the adhesiveness of the viscid spiral by diluting or washing away the sticky droplets.

Contrary to other orb-web spiders, *Cyrtophora* does not remove its web during heavy rain. *Cyrtophora* webs are capable of withstanding such rains with no signs of damage. The census of web renewal frequency cited above partly overlapped the peak rainy season in Wau. Total monthly rainfall and maximum daily rainfall for this period (1970-1971) were:

	Total (in.)	Max./Day (in.)
November	11.09	2.66
December	12.62	2.06
January	12.00	3.60
February	4.07	0.76

Rainfall data are from New Guinea Goldfields Compound No. 1 (altitude 3500 ft.). No correlation could be found between heavy rainfall and web renewal in *C. moluccensis*. One abandoned web was followed for three weeks during this period and showed no appreciable damage due to heavy rains.

Frequency of recurrence and duration of rainfall may be as important here as rainfall intensity. In a wet tropical climate such as that of Wau, days of rain may outnumber days of no rain, and during wet seasons, rains may continue unabated for several hours. Unlike typical orb-webs, the *Cyrtophora* web can continue to function as a trap throughout these periods. Many insects (e.g., moths, winged ants, some beetles) were particularly active during or immediately following moderate to heavy rainfall (Lubin, in preparation). *Cyrtophora* can exploit these food resources, while other orb-weavers must first rebuild their webs to do so.

A similar argument applies to the effects of wind on webs. However, no data are available on the actual response of spider webs to high wind velocities. Langer (1969) suggested that webs that are stretched during high winds may not undergo complete elastic return, and would remain slack. They would then have greater accelerations and larger excursions in a wind and be more likely to rupture. Langer also points out that thread slackness would reduce the efficiency of signal transmission in the web. A close-meshed, vertical web would produce greater drag than an open-meshed web and, assuming the main component of the wind to be horizontal, the more inclined the web, the less drag it will produce. Therefore, large vertical close-meshed webs should not be found in areas subject to high winds.

Most orb-weavers construct their webs in somewhat sheltered areas. *Nephila maculata*, with its large vertical web of relatively fine mesh, tends to build in forest understory and near trees or other sheltered areas in clearings. Many araneids found in open grasslands build small, low-energy webs that must be renewed several times a day if conditions are adverse. *Cyrtophora*, to the contrary, is able to maintain a large, close-meshed web in the most exposed areas. As in the case of resistance to heavy rains, the *Cyrtophora* web can probably withstand strong winds due to a) thread strength, b) the 3-dimensional structure, with its large number of connections to surrounding supports, and c) the horizontal position of the close-meshed orb and the open, irregular structure of the barrier webs.

Cost of Web-Building

The energy contents of an entire *C. moluccensis* web, of the renewed portion, and of an entire *N. clavipes* web are given in Table 6, along with other web parameters and body weights of the spiders. The cost of the web is expressed both as the energetic cost for the whole spider, and as the energetic cost per gram body weight. The cost of a complete *C. moluccensis* web is about 2 1/2 times that of a *N. clavipes* web (on a per gram basis). However, the cost of the renewed portion of a *C. moluccensis* web is less than one tenth that of the entire web.

Cyrtophora moluccensis builds a complete web only once in its adult life and renews approximately 10 percent of it every 18 days. Thus, its total energy expenditure in web building during its adult life is (in cal. per gram body weight):

$$578.8 + (T_1/18)\ 47.9 = 578.8 + 2.7T_1$$

where, T_1 = adult life span in days.

Table 6 Body weight, web parameters and cost of web-building in *C. moluccensis* and *N. clavipes*. (± standard deviation)

	Body Wt (g)	Web Size (cm)	Dry Wt. of Web (g)	Energy Content of Web (cal.)	Web Energy Content/ Body Wt. (cal /g.)
C. moluccensis Whole Web	1.37 ± .35	64.2 x 59.9	174 (n = 1)	792.9	578.8
C. moluccensis Removed part of web			0.10 ± .001 (n = 3)	65.6 ± 3.5	47.9
N. clavipes	.91 ± .31	55.5 x 51.3	.046 ± .02 (n = 4)	208.4 ± 120.1	229.0

Nephila clavipes renews its entire web every three days (approximately 1/3 of the web is renewed daily), thus, its total energy expenditure in web-building during adult life is:

$$229.0 + (T_2/3)\ 229.0 = 229.0 + 76.3T_2$$

Cyrtophora moluccensis has a large initial outlay of energy in building a complete web, but subsequent web renewals are energetically inexpensive. The low cost and infrequent occurrence of web renewal may partly explain why *Cyrtophora* discards rather than ingests the old web. *Nephila clavipes*, on the contrary, has a smaller initial expenditure, but subsequent web renewal requires much greater energy expenditure than in *C. moluccensis*. It is also evident that the longer the adult life spans of the spiders (T_1 and T_2), the greater the energetic advantage *Cyrtophora* has over *Nephila*. Detailed data on adult life spans of *C. moluccensis* and *N. clavipes* are unavailable. The average adult *C. moluccensis* life span was estimated at 3 1/2 months, and two adult female *C. moluccensis* in a study colony were observed for over 5 months, the longest known record of *N. maculata* is about 4 months (Robinson and Robinson, unpublished).

These calculations have not included the cost of daily web repairs in *C. moluccensis*, nor the metabolic cost of web-building activities. The cost of daily web repairs could not be estimated, it is assumed, however, to be very small (see page 29). The metabolic cost of web-building activity may be calculated from the active metabolic rate and the average duration of web-building. Average metabolic rates, used as estimates of active metabolic rates, are

2.9 cal./hr. (S.D. = 0.9, n = 13) for *C. moluccensis*, and 1.4 cal./hr (S.D. = 0.6, n = 12) for *N. clavipes*. Approximate durations of web-building activity are *C. moluccensis*, whole web - 12 hours, *C. moluccensis*, renewed part - 6 hours, and *N. clavipes*, whole web - 4 hours. Based on these figures, the energy expended in web-building activity would be

C. moluccensis, whole web - 34.8 cal.
C. moluccensis, renewed part - 17.4 cal.
N. clavipes, whole web - 5.6 cal.

These estimates, as mentioned earlier, may be subject to considerable error. As these figures are small, and in fact do not substantially change the original calculations based on the energy content of the web alone, they may be ignored.

Note also that the time loss in web renewal is greater for *Nephila* than for *Cyrtophora*, *Nephila* loses approximately 4 hours every 3 days in web renewal, while *Cyrtophora* loses only 6 hours every 2 1/2 weeks. Daily repairs do not hamper the trapping ability of the *Cyrtophora* web, and the spider continues to respond to prey while repairs are under way.

Conclusions

The 3-dimensional, knockdown web of *Cyrtophora* is a high cost, relatively inefficient trap for flying insects. However, a series of adaptations, namely, increased web durability and strength, low frequency of web renewal, and reduced energetic cost of web renewal and repair may enable *Cyrtophora* to exploit habitats and food resources that are unavailable, or only partially available, to other orb-web spiders.

Tropical grasslands and savannas are inhabited by several small and for the most part, non-aggregating species of *Cyrtophora*. *Cyrtophora monulfi*, *C. cicatrosa* and an unidentified species (*Cyrtophora* "sp. D") were all commonly found in grassy clearings and fields in the vicinity of Wau, New Guinea. Co-existing with these species are other araneids such as *Cyclosa*, *Araneus* and *Argiope* species. However, while these araneids build low-energy, short-lived webs that require frequent recycling, *Cyrtophora* species maintain a persistent web and can utilize the full range of flying insects available throughout the day and night. They may also exploit insect emergences during and after heavy rains. In many of these respects, the behavior of *Cyrtophora* is similar to that of space-web building theridiids: the web is a more or less permanent, all-weather structure that may be added to and repaired periodically, thus enabling prey capture activities to continue unaffected by environmental conditions. The evolution of colony formation in the two largest species, *C. moluccensis* and *C. citricola*, is considered a logical conclusion to the trend toward exploitation of large, open spaces. This will be discussed in Chapter 4.

Summary

The comparison between the knockdown web of *Cyrtophora* and the sticky web of *Nephila*, may be summarized as follows:

1. Due to the lack of a viscid spiral, the *Cyrtophora* web is a less efficient trap (per unit time) than the *Nephila* web.

2. The *Cyrtophora* web is more permanent and durable than the *Nephila* web. It can, therefore, function as a trap over a longer period of time, and in conditions that are adverse to typical orb-webs.
3. The initial cost of a *Cyrtophora* web is greater than that of a *Nephila* web. However, the cost of maintenance and renewal during the adult lifetime is considerably less in *Cyrtophora*.

Climatic forces, such as heavy rainfall and winds, have probably encouraged the evolution of the non-sticky, knockdown web of *Cyrtophora*. This was done at the expense of a reduction in trapping efficiency and a greater initial energy expenditure required for web-building. Compensating for these losses are increased web durability and trapping time and low web maintenance costs. These adaptations have allowed *Cyrtophora* species to successfully exploit open habitats such as tropical grasslands and savannas.

CHAPTER 3: PREDATORY BEHAVIOR

Introduction

Considerable information is now available on the predatory behavior of orb-web spiders (Peters, 1931, 1933, Robinson, 1969, Robinson et al., 1969, Robinson and Olazarri, 1971). Several consistent patterns of predatory behavior have been detected, and a scheme for the evolution of some of these has been proposed (Robinson et al., 1969). Similarity between predatory behaviors may suggest affinities between orb-web spiders, but it may not be sufficient to indicate exact evolutionary relationships. It was thought that Cyrtophora species, having an unusual web structure, might also have specialized predatory behavior. But if similarities with predatory behaviors of other araneids could be detected, these in turn, might shed light on the evolution of the Cyrtophora web. To this end, a study was undertaken of the prey capture behavior of Cyrtophora.

The study concentrated mainly on the functions and variability of predatory behavior patterns within the genus Cyrtophora. Mechanisms, or causation, and adaptive values of these behaviors were not tested in most cases, and are, therefore, largely speculative. General knowledge of the biology of these species and detailed studies of the feeding habits of prey of C. moluccensis in nature (Lubin, in preparation) have aided in interpreting the functions and adaptive values of many predatory behavior patterns.

Robinson and Olazarri (1971) divided the prey capture behavior of araneid spiders into 5 functional stages:

1. Detection and location of prey.
2. Discrimination of prey type.
3. Prey immobilization.
4. Transportation of prey to the feeding site.
5. Manipulation of prey and feeding.

I have emphasized the patterns of prey immobilization and transport to the hub, as a great deal of variation occurs in these behaviors. Since the behaviors associated with prey detection and location, and discrimination of prey type are not easily discerned, these aspects are treated less thoroughly.

Materials and Methods

Four species of *Cyrtophora* were used for predatory behavior analyses: *C. citricola*, *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Details of size, habitat and study locations of these species are given in Table 7. All species concerned have similar web structure, as described for *C. moluccensis* in the previous chapter. *Cyrtophora monulfi* has, in addition, a conical, silken retreat above the hub, where it rests during the day. *Cyrtophora citricola* occasionally builds a retreat of dead leaves in the upper barrier web above the hub (Kullmann, 1958).

Live insects of various types were presented individually to adult female spiders. Insects tested were blowflies, fruitflies, moths and butterflies, katydids, grasshoppers, dragonflies, large scarab beetles, and weevils. These were not identified taxonomically

Table 7. Comparison of size and habitat of four species of Cyrtophora.

	Study Location	Length (mm)	Weight (g) ± S.D.	Habitat
C. citricola (Forskal)	Ghana, Madagascar Ivory Coast	15 (Levi and Levi, 1968)	no data	Wooded savanna, cacti and ornamentals near human habitation. Generally colonial
C. moluccensis (Doleschall)	New Guinea	20 to 28 (Chrysanthus, 1959)	1.183 ± .415 n = 33	Clearings and disturbed areas, especially near human habitation, araucaria and pine trees, fences telephone wires and ornamental shrubs and trees. Colonies or small aggregations.
C. cylindroides (Walck.)	New Guinea	15 (Chrysanthus, 1959)	.326 ± .14 n = 27	Araucaria plantations, low and mid-altitude rainforest. Solitary.
C. monulfi (Chrysanthus)	New Guinea	8 to 10	.058 ± .015 n = 10	Savanna, fences and low shrubs. Aggregations, but not colony forming.

but in most cases (exceptions were moths, butterflies and grasshoppers) insects within a category were of the same species. A weight range was established for each category of prey. All insects tested on *C. moluccensis*, *C. cylindroides* and *C. citricola* came from habitats in which the spiders themselves were found. The natural prey of *C. moluccensis* included insects from all the above categories (Lubin, in preparation). The insects tested on *C. monulfi* were probably less representative of its natural prey, which may be restricted to small grassland species.

All investigations on *C. citricola*, *C. monulfi* and *C. moluccensis* were performed on field populations. *Cyrtophora citricola* individuals were tested at three locations: a savanna/roadside population in the vicinity of Legon, Ghana; a wooded savanna population at Lamto, in the interior of the Ivory Coast, and several colonies in the O.R.S.T.O.M. Zoological and Botanical Gardens near Tananarive, Madagascar. Studies on *C. moluccensis* and *C. monulfi* predatory behavior were conducted on populations in the vicinity of Wau and Bulolo, New Guinea. *Cyrtophora cylindroides* females were collected from mature araucaria plantations near Bulolo, and kept in screened wooden cages (18 x 18 x 24 in.). Of the *Cyrtophora* species studied, only *C. cylindroides* readily built webs in cages. This was a fortunate coincidence, as individuals in the field were both widely dispersed and located in places where they would have been difficult to study in situ (e.g., high in araucaria branches).

In testing spiders with various insects, I alternated the different types of prey, and in no case was a spider tested with more than one prey per day. However, with the exception of the caged *C. cylindroides*, I had no record of the previous prey of the experimental animals. It is possible that some of the variation observed in predatory responses is a result of the previous experiences of these spiders.

Predatory behavior patterns were analyzed in terms of their smallest, functional units. Commonly occurring sequences of these behavior units were established for each of the four species. Predatory sequences and durations of behavior units within a sequence were recorded for each prey capture incident. Super-8 mm films were made of predatory sequences of *C. moluccensis*, *C. cylindroides*, and *C. monulfi* with a variety of prey. Descriptions of behavior units are based partly on analyses of these films, and partly on direct observation. The terminology and methods of description and analysis of behavior sequences are similar to those used by Robinson and Olazarri (1971). Whenever possible, I have compared behavior units and sequences of predatory behavior of *Cyrtophora* with known predatory behaviors of other orb-weavers.

Cyrtophora Predatory Behavior

A general description of the prey capture behavior of *Cyrtophora* is given below, based mainly on the behavior of the three larger species *C. moluccensis*, *C. citricola* and *C. cylindroides*. Differences in behavior between the four species studied will be detailed later.

The spider rests at the hub or in the retreat (*C. monulfi*). A flying insect striking the upper barrier web either drops onto the horizontal net or remains entangled in the barrier web. The prey produces vibrations in the web upon impact and/or during struggling, and these are transmitted via web elements to the hub (Walcott, 1963). It is possible that some discrimination of prey type on the basis of vibration frequencies occurs at this stage (Walcott and Van der Kloot, 1959; Robinson and Olazarri, 1971). Location of prey in the web often involves plucking the net or threads of the upper barrier web with the first pair of legs.

If the prey falls on the net, the spider runs out to it along the undersurface, and in many instances, touches it with legs I and/or with the palps before attacking. Chemoreceptors and tactile receptors abound on the tarsi and palps of araneid spiders (Foelix, 1970a, 1970b), suggesting that discrimination of prey type may occur at this stage as well. Peters (1933) and Robinson (1969) obtained evidence for tactile discrimination at this stage by showing that after prolonged touching and palpating, *Araneus diadematus* and *Argiope argentata* could distinguish between insects pre-wrapped in silk and unwrapped insects. Insects are immobilized by biting or by wrapping in silk, or by a combination of the two methods. If an insect remains caught in the upper barrier web, the spider runs out under the net and shakes it violently until the prey falls on the net. Insects that cannot be dislodged in this manner are attacked and immobilized in the upper barrier web. The barrier web may be reached by climbing through the open hub, climbing over the outer edge of the net, or by cutting a hole in the net and climbing through it. Insects are rarely attacked in the lower barrier web.

After immobilization, prey are pulled out or cut out of the net or barrier web with the chelicerae. Post-immobilization wrapping at the capture site, and/or biting and manipulation of prey may occur at this stage. In some instances, the spider may rest under or near the prey and clean her palps, chelicerae and legs prior to transporting the prey to the hub. Prey are carried to the hub on the under-surface of the net in the spider's jaws (= chelicerae), or dangling from the spinnerets on a silk thread.

Prey carried to the hub on silk are generally suspended at the hub by a thread, or wrapped (post-immobilization wrap at the feeding site) and suspended. Insects that are carried in the jaws are retained in the jaws, or wrapped and suspended at the hub. Pre-feeding manipulation of prey and actual feeding occur at the hub.

As noted previously by Kullmann (1958), *Cyrtophora* species do not leave a dragline behind them while moving under the net. This is unlike all other araneids, which maintain dragline connection with the hub during prey capture.

Description of Behavior Units

Resting Positions

Several resting positions occur in the species studied.

Rest under hub

The spider rests under the hub, with all legs in contact with the horizontal net. *Cyrtophora cylindroides* always rests in this position, as do *C. moluccensis* and *C. citricola* individuals that lack egg-cases. *Cyrtophora citricola* and *C. moluccensis* females with active egg-cases assume a modified rest-under-hub posture, in which legs IV touch the egg-case (Figure 7). This position is assumed at night and during part of the day. When resting under the hub, the spider is

Figure 7. Rest-under-hub position of *C. moluccensis* female with egg-case.

in maximum contact with the horizontal net and is probably in the optimum position for receiving web vibrations.

When disturbed, *C. citricola* assumes an interesting cryptic position which involves pulling all the legs inward toward the body, thereby obscuring the typical spider-like outline. Another small, unidentified species of *Cyrtophora* in New Guinea (sp. "D"), has a similar cryptic resting position.

Cyrtophora monulfi leaves its retreat and rests under the hub at night, presumably when its predatory activity is most intense and when the danger from visually orienting predators is least.

Rest under egg-case

Cyrtophora citricola and *C. moluccensis* females with egg-cases assume a resting posture under the egg-case throughout most of the day (Figure 8) In this position, the last two or three pairs of legs rest on the egg-case, while legs I or legs I and II touch the horizontal net or threads of the barrier web above the hub. Contact with the egg-case is maximal in this position, but the spider may be less capable of receiving stimuli from prey in the web. Some observations suggest that spiders resting under an egg-case may be slower in responding to prey.

Cyrtophora cylindroides females with egg-cases were never observed in this posture

Rest in retreat

Of the species studied, only *C. monulfi* consistently builds a retreat and rests in it during the day. The retreat is conical, with the open end facing downward toward the horizontal net, and made

Figure 8. Rest-under-egg-case position of _C. moluccensis_ female.

entirely of silk. The spider can close off the open end of the retreat by pulling the lower edge inward with legs I, this is the position shown in Figure 9. Normally, however, the retreat is open and the spider rests in it with legs I touching the threads of the barrier web above the hub. Vibrations in the web are detected by the spider even when in its retreat. The egg-cases are suspended from the edge of the inner wall of the retreat and are well camouflaged (Figure 9).

Hang at hub

During midday, when the sun is high, individuals of *C. moluccensis* hang from the hub by legs IV, or III and IV (Figure 10). Spiders position themselves so that the dorso-posterior side receives the maximum insolation, while the rest of the body is shaded. In this position the spider may be exposing a minimal surface area to the sun. When mirrors and shades were used to change the direction and angle of insolation, the spider re-oriented to maintain its original position with regard to the "new" sun. Positioning with respect to the sun's rays has been described in *Nephila clavipes* in Florida (Krakauer, 1972), in *N. maculata* in New Guinea (Robinson and Robinson, unpublished), and in the linyphiid *Frontinella communis* (Pointing, 1965), and strongly suggests the presence of behavioral regulation of body temperature. Krakauer showed that *N. clavipes* responds to heat-lamp radiation in the laboratory in a manner similar to its positioning on the web in response to direct sunlight. Behavioral thermoregulation has been studied in several heliothermic insects, including cicadas (Heath, 1967, Heath and Wilkin, 1970), dragonflies (Hardy, 1966), butterflies

Figure 9 Retreat of *C menulfi* with egg-case attached to lower edge.

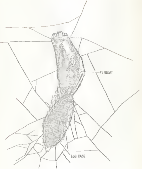

RETREAT
EGG CASE

Figure 10 Hang-at-hub (sun avoidance) position of *C moluccensis*. Arrow indicates direction of sun's rays.

(Clench, 1966) and locusts (Waloff, 1963). Mechanisms for increasing heat loss or reducing heat gain may occur commonly in terrestrial invertebrates that face regular, high radiant heat loads. *Cyrtophora moluccensis*, with its typically exposed web, is most certainly included in this category.

Cyrtophora monulfi and *C. cylindroides* were not seen to hang from the hub. As *C. monulfi* rests in a retreat during the day, it may have no need for special sun-avoidance behavior. *Cyrtophora cylindroides* is a shade-dwelling forest species and it is likely that its webs never receive direct sunlight. The average midday temperature in a stand of 35-year-old *Araucaria cunninghamii* where *C. cylindroides* webs were found was considerably lower than in the surrounding open fields or at the plantation edge where *C. moluccensis* webs were located (R. Wiley, personal communication).

Cyrtophora moluccensis assumes a hang or hub position during heavy rainfall. Unlike *Nephila maculata* (Robinson and Robinson, unpublished), *C. moluccensis* does not cut out sections of its web during rain or move into the nearby vegetation. Presumably, by hanging at the hub, the spider presents a minimal surface area to the rain, thereby reducing its impact. *Argiope argentata* was also observed to hang from the hub during heavy rain (Robinson and Robinson, unpublished) and it was suggested that the outstretched legs I and II act as a drip-tip, enabling the water to flow off the spider's body. *Cyrtophora monulfi* does not hang at the hub in response to rain, and data on *C. citricola* and *C. cylindroides* are unavailable.

Plucking

Plucking has been observed in all species studied (though not necessarily in all predatory sequences) and consists of a rapid jerking of the radii with legs I. Plucking may occur in response to movement in the web, or upon return to the hub after prey capture. In the latter case, the spider may turn in a circle at the hub, plucking the net at intervals as it turns. It may pluck threads of the upper barrier web as well. A low intensity tensioning of the web may also occur in response to prey in the web. Tensioning involves a slow pulling inwards of the radii with legs I and II.

It is not clear what stimuli trigger plucking or tensioning; two possibilities are the weight of the prey in the web and vibrations detected through web elements. In either case, plucking may be a means of precise location of objects in the web. Due to the large number of radii and spiral connections in a *Cyrtophora* web, signal transmission may be somewhat diffuse. Plucking would put greater tension on the radii, thereby enabling the spider at the hub to locate objects in the web. Robinson and Olazarri (1971) observed that plucking behavior in *Argiope argentata* was most pronounced when prey did not struggle in the web. They suggested that plucking is a method of accurately locating non-vibrating prey in the web. Earlier, Barrows (1915) proposed that radii in contact with prey would vibrate at a different frequency and that the spider could spatially compare the echo vibrations after plucking from unloaded and loaded radii. The mechanism of prey location by plucking deserves investigation.

Like other araneids, *Cyrtophora* may also pluck the web as it approaches the prey. This probably allows for corrections in the spider's orientation toward non-vibrating prey. I have never observed *Cyrtophora* to "err" in the directional location of prey in the web. Occasionally, however, mistakes are made in distance location and the spider "over-shoots the mark." This seems to occur most often with small, rapidly vibrating prey, such as buzzing blowflies, which elicit a very rapid attack. Robinson and Robinson (unpublished) observed this in *Nephila maculata*, particularly with blowflies and dragonflies as prey.

A great deal of plucking takes place with prey attacked in the upper barrier web. It is possible that signal transmission through the irregular barrier web is less accurate than through the net, making prey location more difficult.

Plucking or tensioning may also enable some discrimination of prey type. Walcott and Van der Kloot (1959) and Walcott (1963, 1969) showed that the vibration receptors of *Achaearanea tepidariorum* (a theridiid) may become more sensitive to different frequencies of airborne vibrations by changing the loading on the tarsus. This is apparently the result of altering tension on the slits of the lyriform organs. If this is true for orb-web spiders as well, then plucking and tensioning may be a method of "tuning in" to characteristic vibration frequencies of insects. More experiments are needed on the sensory aspects of prey discrimination in spiders.

Web Shaking

This involves sudden and large amplitude shaking of the horizontal net with legs I or legs I and II. Web shaking is quite distinct from plucking, as it is a vertical motion rather than the horizontal pull and release characteristic of plucking. Web shaking occurs in the following situations:

a. if an insect is caught in the upper barrier web, the spider runs out under the net until it is beneath the prey and shakes the net. This may be repeated many times until the prey is dislodged from the barrier web and drops on the net.

b. Theridiid kleptoparasites often approach a spider feeding at the hub, apparently in an attempt to steal prey. In such instances, the spider may shake the net at or near the hub, thereby chasing away the intruders. Similar behavior occurs during intraspecific aggression in *C. moluccensis* and *C. monulfi* (Chapter 4).

c. *Cyrtophora moluccensis* egg-cases are parasitized by a sarcophagid fly. The wingbeat vibrations of this fly elicit web shaking in adult *C. moluccensis* females. The anti-parasite behavior of *C. moluccensis* is discussed in Chapter 4. This has not been observed in other species of *Cyrtophora*.

Web shaking of the sort that occurs in *Cyrtophora* species does not seem to occur in other araneids. *Nephila clavipes*, juvenile *N. maculata*, and *Argiope* and *Araneus* species shake their webs when disturbed by a large object, but these appear to be higher frequency vibrations whose function may be to obscure the spiders' outline. It is possible that web shaking in *Cyrtophora* is related to this type of anti-predator web vibrating behavior.

Prey Immobilization

Biting

Immobilization by biting occurs commonly in all species of *Cyrtophora* studied. The prey is initially grasped with legs I, II, and III, and the spider appears to bite the nearest or most readily accessible part of the insect's body. If this is a wing or a leg, the spider then moves down to a more "substantial" part of the insect's body, e.g., the base of an appendage, thorax or abdomen. Similar behavior was observed in *A. argentata* (Robinson and Olazarri, 1971). Most prey are held in legs III, or II and III, during the bite.

Prey that are immobilized by wrapping may be bitten after the wrap (post-immobilization bite at capture site). As pointed out by Robinson and Olazarri (1971) for *A. argentata*, the post-immobilization bite is generally directed toward the anterior portion of the insect's body. The cues that trigger biting after a wrap-restraint are not entirely known, but may involve detection of the silk coating (Peters, 1931; Robinson, 1969)

Prey with hard exoskeletons, such as most beetles, may be given a number of short bites during immobilization wrapping. These are probably exploratory bites, rather than actual penetration through the cuticle and injection of venom. The nocturnal araneid *Eriophora fuliginea* (Robinson *et al.*, 1972) and *N. maculata* (Robinson and Robinson, unpublished) also repeatedly attempt to bite coleopterans. In both instances, the authors noted that penetration through the hard exoskeleton was unlikely and one could actually hear the clicking of the chelicerae as they glanced off the smooth elytra. Short, exploratory bites may also be given to prey by *Cyrtophora* after it is removed from the net, prior to transport to the hub. Rapid "bite and back off" sequences were not observed in *Cyrtophora*, though they are common in other araneids such as *Gasteracantha* and *Nephila*.

Wrapping

Prey may be wrapped at several stages of the predatory sequence (Robinson *et al.*, 1969):

a. Immobilization wrapping. Insects are attacked and partly or completely immobilized by wrapping in silk.
b. Post-immobilization wrapping at the capture site. Prey that were immobilized by biting or by wrapping, may be wrapped prior to transportation to the hub.
c. Post-immobilization wrapping at the feeding site. Prey may be wrapped at the hub prior to feeding.

In the wrap immobilization, silk is thrown out under the net in broad sheets with legs IV. Often the spider approaches the prey, and turning 90° to 180°, faces away from the prey and begins throwing sheets of silk in an upward and slightly posterior direction. Facing away and throwing behavior was observed most frequently in attack sequences on pentatomids and large acridids or tettigoniids presented to *C. moluccensis* and *C. cylindroides*. Similar behavior was observed in *A. argentata* (Robinson and Olazarri, 1971) and to a much greater extent in the nocturnal *Eriophora fuliginea* (Robinson *et al.*, 1972). In all wrap restraints, silk is initially thrown upwards from a distance. There is no actual bodily contact with the prey.

Initial throwing of silk does not always immobilize actively struggling prey. Silk swathes thrown upward onto the net may temporarily restrain prey by catching appendages protruding through the net. The spider may then rapidly bite a hole in the net and resume throwing silk onto the prey as it drops through the hole. When the prey is thus partly immobilized, wrapping behavior changes gradually from throwing to the application of swathes of silk directly to the surface of the prey. Close contact wrapping is typical of wrapping after the initial restraint (post-immobilization wrapping).

Two phases of post-immobilization wrapping may be distinguished: wrapping of prey still caught on the net, and wrapping of prey hanging in the free zone beneath the net (free wrapping). During the initial phase, the spider sits below the prey, holding it with legs II and III, while legs IV alternate in pulling out and applying swathes of silk directly onto the prey. In the case of insects restrained by biting, or by wrapping and biting, wrapping usually begins while the prey is still in the spider's jaws.

As the prey is freed from the net by pulling out or by cutting out, the first phase of wrapping merges into the second. The spider retains its hold on the net with one leg I (or with leg I and II) while grasping the prey with the remaining legs I, II, and III. The prey is suspended from the net by one or two threads. The spider is, thus, oriented perpendicular to the long axis of the prey and begins to rotate the prey with legs I, II and III and with the palps, while applying silk over the prey in a forward motion with legs IV. Legs I, II and III pull the anterior edge of the prey toward the spider's body, while legs IV push the posterior edge away from the body (see Robinson and Olazarri, 1971, p. 9). The prey is thus rotated toward the anterior of the spider and silk is wound onto the prey, much like winding thread onto a spool. This behavior was previously described in *A. argentata* (Robinson and Olazarri, 1971) and in *E. fuliginea* (Robinson *et al.*, 1972). The prey of *Argiope* and *Eriophora*, however, is supported on a radius of the orb-web, while that of *Cyrtophora* hangs beneath the net. Like *Argiope*, *Cyrtophora* moves its abdomen in an arc from side to side as silk is pulled out with legs IV. In this manner, a large area may be covered evenly with silk.

Large, bulky prey are wrapped in a manner that may reduce their bulk. When wrapping dragonflies, for example, the wings and long abdomen of the dragonfly are pulled inward and wrapped together. The resulting prey package is of more manageable size and may be cattled with less risk of entanglement in the web.

Post-immobilization wrapping may occur at the hub, and during transport to the hub. Wrapping during transport occurs mainly when prey become caught in the net or in the lower barrier web. Occasionally, prey that are transported in the jaws are wrapped part way to the hub and transferred to the spinnerets.

Insects that are restrained in the upper barrier web may be wrapped in the same manner as those immobilized on the net. A second wrapping generally occurs under the net (free wrap), prior to transport to the hub.

Pulling Out and Cutting Out

Small prey may be pulled out of the net with the chelicerae. The spider pulls the prey down with the jaws and legs III, while legs I and II push against the net. *Cyrtophora* attempts to pull out most prey that are bitten at the capture site (either immobilization or post-immobilization bite), including large prey that are subsequently cut out of the web. Pulling out seems to follow biting in the normal sequence of prey capture behavior, but is successful only with small, compact prey such as fruitflies and blowflies. Difficulty in pulling prey out of a Cyrtophora web is due to web strength and fineness of the mesh, rather than web adhesiveness, as in the case of typical orb-weavers.

Pulling out behavior may also be a method of testing the condition of prey that have been immobilized by biting, without loosening the grip on them. Since insects do not actually adhere to the net, the possibility of escape from a Cyrtophora web due to incomplete immobilization is greater than from webs of other araneids (see Chapter 2). There would be an advantage, therefore, to testing prey immobility prior to releasing them.

Most prey, other than very small insects, are removed from the net by a combination of alternately cutting out and pulling down with the legs and jaws. In cutting out, threads of the net or upper barrier web in immediate contact with the prey are cut with the chelicerae, while the prey is pulled down with legs I, II, and III. The functional distinction between cutting out and pulling out is less clear in Cyrtophora species than in A. argentata (Robinson and Olazarri, 1971). Nor is there a definite temporal sequence of cutting spiral and radial web elements, as in Argiope. This is understandable, as there is no difference in physical properties between these elements in a Cyrtophora web. In all likelihood, the combination of cutting and pulling is simply a method of freeing prey with the minimum amount of damage to the net. Pulling out results in the least damage; cutting and pulling out results in a small hole, approximately the diameter of the insect as it is pulled through the net head first.

With insects that are immobilized entirely by wrapping, cutting out may occur as part of the wrap sequence, during the transition from restraint wrapping to free wrapping under the net.

Transportation to the Hub

Carry in jaws

Small prey are often carried to the hub in the chelicerae. An insect may be wrapped at the capture site and transferred to the jaws for transport, retaining a swath of silk connecting it to the spider's spinnerets. Small prey that are seized and pulled out with the jaws are generally carried to the hub in the jaws without prior wrapping.

Carry on silk

Most prey are carried to the hub dangling on a thread from the spinnerets. The spider's abdomen is oriented horizontally under the net, and the wrapped prey package hangs down over the posterior edge of the abdomen. Prey are always supported with one or both legs IV during transport. This may prevent prey from swinging from side to side and becoming entangled in the lower barrier web. *Araneus diadematus* and *Argiope argentata* also support prey packages with legs IV (Peters, 1931, Robinson and Olazarri, 1971), but *A. argentata* may carry prey without support.

All prey, whether carried on silk or in the jaws, are transported to the hub on the under-surface of the net. Unlike other araneids, *Cyrtophora* does not produce a dragline during prey capture, and all movements, including transport of prey to the hub, take place on the net itself.

Manipulation at the Hub

Prey carried on silk are suspended at the hub. Upon reaching the hub, the spider pulls down on the thread from which the prey is suspended with one leg IV, thus pulling out a length of thread, and then dabs the spinnerets onto the net. The spider then turns 180° and pulls the prey up to the chelicerae with legs I and II. In the act of dabbing the spinnerets to the net, the silk line is cut with the aid of leg IV. It is unclear whether the thread is cut by the leg itself, or by some cut-off mechanism in the spinnerets. As yet, no evidence of a cut-off valve has been found in araneid spinnerets (Wilson, 1969).

Prey are manipulated with the palps, chelicerae, and legs I and II prior to feeding. Feeding generally occurs at the anterior end of the prey. During feeding most prey are held in the jaws alone, and the spider resumes a resting position with all legs under the web. Large prey may be held with legs III; occasionally, Cyrtophora feeds in a hanging position with legs I, II, and III grasping the prey and legs IV holding onto the hub. The latter position would undoubtedly reduce the spider's ability to receive web vibrations. The feeding behavior of araneids is insufficiently known to allow speculation on the adaptive value of feeding postures.

Description and Analysis of Behavior Sequences

Attack Sequences

Attack sequence is used here to denote prey immobilization and subsequent behavior up to transportation of the prey to the feeding site. Analysis of *Cyrtophora* prey capture sequences with various types of insect prey revealed four basic attack sequences:

1. wrap/bite/pull, cut out/free wrap
2. wrap/cut out/free wrap
3. bite/wrap/cut out/free wrap
4. bite/pull out (or cut out)

Two of these sequences involve immobilization by wrapping, and two immobilization by biting. Tables 8 to 11 give the frequency of occurrence of each attack strategy in four species of *Cyrtophora* with different insect prey. Other, less common attack sequences are listed under a fifth, non-specific category. Tables 12 to 14 show the durations of behavior units within sequences for *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Durations are given only for the most commonly occurring sequences with each prey type.

Post-Attack Sequences

Post-attack sequences involve transportation to the hub and manipulation of prey at the hub. The two basic methods of transportation, carry-in-jaws and carry-on-silk, have already been described. Frequencies of occurrence of these two methods in behavior sequences with different prey types are shown in Tables 15 to 18. Durations of post-attack sequences and total sequence durations are shown in Tables 12 to 14.

The following discussion will concentrate on the variation in sequences of attack and transportation that occur with different prey and their possible adaptive values. Comparisons made with *A. argentata* and *E. fuliginea* are based on data from Robinson (1969), Robinson and Olazarri (1971) and Robinson *et al.* (1972).

Table 8. Frequency of occurrence, in percent, of different attack sequences in C. *molecensis*.

Attack Sequence	Moths n = 24 25-150 mg	Blowflies n = 25 50-60 mg	Stratiomyids n = 30 100-120 mg	Grasshoppers and Katydids n = 29 100-175 mg	Dragonflies n = 26 c. 150 mg	Weevils n = 19 c. 35 mg	Scarabs n = 13 500-1000 mg
wrap/bite/pull, cut out/free wrap	8.3	no	36.7	20.7	26.9	31.6[1]	92.3[1]
wrap/cut out/ free wrap	no	4.0	30.0	44.8	15.4	63.1	7
bite/wrap/pull, cut out/free wrap	83.4	76.0	30.0	31.0	57.7	no	no
bite/pull out (cut out)	8.3	20.0	no	no	no	no	no
other	no	no	3.3	3.5	no	5.3	no

[1] modified sequence, see text

Table 9. Frequency of occurrence, in percent, of different attack sequences in *C. citricola*.

Attack Sequence	Moths and Butterflies n = 21	Blowflies n = 22	Fruitflies n = 20	Grasshoppers and Katydids n = 18
wrap/bite/pull, cut out/free wrap	no	4.5	no	33.4
wrap/cut out/ free wrap	9.5	no	no	22.2
bite/wrap/pull, cut out/free wrap	81.1	86.5	no	22.2
bite/pull out (cut out)	9.5	4.5	100.0	no
other	no	4.5	no	22.2*

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* Test bite/back off/wrap.

Table 10. Frequency of occurrence, in percent, of different attack sequences in _C_ _cylindroides_

Attack Sequence	Moths n = 20 50–125 mg	Blowflies n = 22 50–60 mg	Katydids n = 25 110–175 mg	Pentatomids n = 20 c. 35 mg
wrap/bite pull, cut out/free wrap	5.0	9.1	12.0	no
wrap/cut out/ free wrap	no	no	20.0	90.0
bite/wrap/pull, cut out/free wrap	95.0	77.3	68.0	no
bite/pull out (cut out)	no	13.6	no	no
other	no	no	no	10.0*

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*Test bites/wrap/cut out/free wrap

Table 11. Frequency of occurrence, in percent, of different attack sequences in *C. menulfi*.

Attack Sequence	Moths n = 25 15-100 mg	Blowflies n = 25 50-60 mg	Pigmy Grasshoppers (Tetrigidae) n = 22 12-15 mg
wrap/bite/pull, cut out/free wrap	no	no	36.5
wrap/cut out/ free wrap	no	no	4.5
bite/wrap/pull, cut out/free wrap	100.0	100.0	54.5
bite/pull out (cut out)	no	no	no
other	no	no	4.5

Durations (in seconds) of attack and transportation to hub, and total durations of prey capture sequences in *C. moluccensis*. Total sequence durations include behaviors not shown under attack and transport

n = no. of prey for which behavior durations
were measured
M = mean
S.D. = standard deviation

Prey and attack sequence		Attack		Transport		
		Wrap	Bite	Cut out/ free wrap	Carry to hub	Total Sequence
Moths (Bite/wrap)	n		20	17	12	18
	M		80.55	48.4	20.3	109.6
	S.D.		63.15	20.2	30.5	111.9
	Range		6-265	21-90	5-118	50-340
Blowflies (Bite/wrap)	n		19	17	14	18
	M		34.8	25.5	7.6	112.5
	S.D.		31.1	14.2	3.0	101.2
	Range		9-130	12-39	3-13	32-377
Stratiomyids (Wrap/bite)	n	11	11	9	7	11
	M	8.2	128.1	52.2	11.6	178.9
	S.D.	5.7	116.2	14.5	10.95	101.2
	Range	2-17	3-420	7-55	5-36	77-412
Stratiomyids (Wrap)	n	9[1]			6	9
	M	26.2			9.5	96.4
	S.D.	9.5			8.5	62.2
	Range	15-47			3-25	22-201
Stratiomyids (Bite/wrap)	n		9	9	5	9
	M		76.2	21.9	9.6	117.1
	S.D.		49.7	7.0	4.3	58.6
	Range		8-156	12-36	4-15	46-218
Grasshoppers and Katydids (Wrap/bite)	n	6[2]	8	4	*	3
	M	13.5	54.2	37.0		195.3
	S.D.	18.8	76.6	10.4		115.3
	Range	0-38	2-207	14-49		69-295
Grasshoppers and Katydids (Wrap)	n	10[1]			6	10
	M	40.0			28.3	101.1
	S.D.	14.95			28.8	88.7
	Range	22-58			9-75	53-323

Table [illegible] (continued).

Prey and attack sequence		Attack		Transport		
		Wrap	Bite	Cut out/ free wrap	Carry to hub	Total Sequence
Grasshoppers and Katydids (Bite/wrap)	n		9	7	5	5
	M		43.8	52.4	5.0	128.2
	S.D.		39.5	46.0	1.9	54.8
	Range		7-135	28-156	3-8	72-191
Dragonflies (Wrap/bite)	n	7[2]	6	7	7	7
	M	12.3	124.2	57.6	12.4	282.4
	S.D.	13.6	159.0	10.5	6.1	217.1
	Range	0-37	44-448	50-78	4-23	128-765
Dragonflies (Bite/wrap	n		15	14	12	14
	M		136.9	51.8	14.9	330.1
	S.D.		133.2	35.0	12.4	149.8
	Range		12-334	16-139	4-40	119-600
Weevils (Wrap/bites)[3]	n	6	5	*	*	6
	M	16.8	67.6			117.2
	S.D.	7.6	72.15			53.7
	Range	9-28	9-184			60-202
Weevils (Wrap)	n	12[1]			6	12
	M	12.45			12.3	36.6
	S.D.	3.1			13.5	34.6
	Range	8-19			2-36	20-123
Scarabs (Wrap/bites/ wrap)[4]	n	12				12
	M	529.1				661.0
	S.D.	374.0				357.2
	Range	57-1395				120-1400

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[1] Durations of wrap and cut out/free wrap lumped together

[2] Some durations too short to be measured accurately

[3] Test bites and manipulation of prey with legs and jaws

[4] Sequence repeated many times

[*] Small sample size

[illegible] 13 Durations (in seconds) of attack and transportation to hub, and total durations of prey capture sequences in *C. cylindroides*. (see Table 12)

Prey and attack sequence		Attack		Transport		Total Sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths (Bite/wrap)	n		19	18	18	19
	M		290.2	55.9	10.0	414.7
	S.D.		167.1	19.3	3.1	160.7
	Range		46–764	23–83	4–15	169–844
Blowflies (Bite/wrap)	n		17	17	16	17
	M		212.65	26.8	10.7	258.2
	S.D.		202.55	16.2	4.2	211.25
	Range		36–653	5–70	5–20	55–767
Katydids (Wrap/Bite)	n	3	3[1]	3	3	3
	M	26.0	25.0	32.3	8.0	164.3
	S.D.	19.2	39.0	26.0	6.1	69.6
	Range	4–39	0–70	7–59	1–12	88–225
Katydids (Wrap)	n	4		4	4	4
	M	29.25		49.5	12.0	179.75
	S.D.	11.7		58.4	4.3	141.5
	Range	14–42		16–137	8–18	76–377
Katydids (Bite/wrap)	n		17	17	13	16
	M		45.6	55.3	12.7	241.4
	S.D.		43.3	36.6	6.8	84.2
	Range		2–151	5–127	4–30	65–361
Pentatomids (Wrap/cut out/rest-clean)[2]	n	18			*	18
	M	161.7				261.2
	S.D.	115.1				171.5
	Range	29–383				44–577

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[1] Some durations too short to be measured accurately

[2] Repetitive sequence, see text

* Small sample size

Table 14 Durations (in seconds) of attack and transportation to hub, and total durations of prey capture sequences in G. mosulfi. (see Table 12)

Prey and attack sequence		Attack		Transport		Total Sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths (Bite/wrap)	n		25	25	20	25
	M		164.4	99.1	37.15	398.6
	S.D.		128.7	41.2	64.1	220.5
	Range		16-457	22-165	2-277	98-785
Blowflies (Bite/wrap)	n		25	23	*	25
	M		118.2	56.0		245.7
	S.D.		108.9	23.2		124.1
	Range		28-545	14-107		111-928
Small Grasshoppers (Wrap/bite)	n	8[1]	8[1]	8	8	8
	M	5.4	30.0	27.0	5.0	155.9
	S.D.	4.9	18.55	7.7	3.2	110.3
	Range	0-16	0-59	11-38	2-11	94-423
Small Grasshoppers (Bite/wrap)	n		12	11	5	12
	M		79.75	38.9	4.2	184.7
	S.D.		92.5	18.0	1.9	109.5
	Range		17-333	17-73	2-7	40-437

[1] Some durations too short to be measured accurately

* Small sample size

Table 15. Frequency of occurrence, in percent, of transport-to-hub sequences in *C. moluccensis*

	Moths n = 24 25-150 mg	Blowflies n = 25 50-60 mg	Stratiomyids n = 30 100-120 mg	Grasshoppers and Katydids n = 28 100-175 mg	Dragonflies n = 26 c. 150 mg	Weevils n = 19 c. 35 mg	Scarabs n = 13 500-1000 mg
Carry on silk	79.2	48.0	76.7	100	100	84.2	100
Carry in jaws	12.5	48.0	23.3	0	0	15.8	0
In jaws + on silk	8.3	4.0	0	0	0	0	0

Table 16. Frequency of occurrence, in percent, of transport-to-hub sequences in *C. citricola*.

	Moths and Butterflies n = 21	Blowflies n = 22	Fruitflies n = 20	Grasshoppers and Katydids n = 18
Carry on Silk	85.7	95.5	5.0	100
Carry in Jaws	14.3	4.5	95.0	0

Table 17. Frequency of occurrence, in percent, of transport-to-hub sequences in *C. cylindroides*.

	Moths n = 20 50-125 mg	Blowflies n = 22 50-60 mg	Katydids n = 25 110-175 mg	Pentatomids[1] n = 17 c. 35 mg
Carry on Silk	95.0	59.1	100	100
Carry in Jaws	5.0	40.9	0	0

[1] No data on three transport sequences.

Table 15. Frequency of occurrence, in percent, of transport-to-hub sequences in *C. moulfi*.

	Moths n = 25 15-100 mg	Blowflies n = 25 50-60 mg	Pigmy Grasshoppers n = 22 12-15 mg
Carry on Silk	100	100	100
Carry in Jaws	0	0	0

Sequences With Moths

Lepidoptera are nearly always immobilized by biting, by all four species of *Cyrtophora*. The third attack sequence, bite/wrap/cut out/free wrap, is the predominant one used with moths and butterflies. Robinson (1969) showed that *A. argentata* immobilizes moths by a long bite, while most other prey are restrained by wrapping. He suggested that since moths can escape readily from sticky webs by shedding the loose scales in contact with the web (Eisner *et al.*, 1964), a rapid restraint by biting would be most advantageous. As the *Cyrtophora* web is non-sticky, scales can be of little advantage in freeing a moth from the web. It is more likely that a moth can slip out of the silk thrown on it during a wrapping attack, and therefore, the bite immobilization and immediate injection of venom is more effective. Robinson (1969) showed that Lepidoptera are recognized by the spider, at least in part, by their surface texture. Other araneids (e.g., *Eriophora fuliginea* and other *Argiope* spp.) which have both wrap and bite immobilization behavior, also use the biting restraint for Lepidoptera (Robinson, personal communication).

A small proportion of "mistakes"—moths attacked by a wrap immobilization sequence—were made by *C. citricola*, *C. cylindroides*, and *C. moluccensis*. This was found to be the case with *A. argentata* as well (Robinson, 1969). Most of these "mistakes" were made with moths attacked in the upper barrier web. These moths were wrapped only a few times (2 to 3 second duration) and immediately bitten. It is possible that discrimination of prey type is more difficult in the barrier web, due to its diffuseness, than under the net. As moths make up a large fraction of the prey of C. *moluccensis* in the area studied (and possibly of the other species as well, Lubin, in preparation), one might expect "mistakes" in the method of attack to be minimized. This appears to be the case: C. *moluccensis* made 8.3 percent "mistakes" with live moths, while A. *argentata* which does not feed on lepidopterans to any large extent, made 17.2 percent "mistakes" with live moths and 16 percent "mistakes" with live butterflies (Robinson and Olazarri, 1971). *Eriophora fuliginea*, a nocturnal araneid which may specialize on moths, wrapped less than 6 percent of the moths (Robinson *et al.*, 1972).

Most moths are wrapped at the capture site and carried to the hub on silk. The larger species, C. *moluccensis* and C. *citricola*, carry a small percentage in their jaws. Some of these, however, are wrapped part way to the hub and transferred to the spinnerets.

Sequences with Flies

Blowflies are immobilized predominantly by biting. Attack sequences 3 and 4 were used on 96.0 percent of the blowflies tested on C. *moluccensis*, 91.0 percent of those tested on C. *citricola*, 100.0 percent of those tested on C. *monulfi* and 90.9 percent of those tested on C. *cylindroides*. Small fruitflies tested on C. *citricola* were always immobilized by biting. Sequence 4, bite/pull out, was used on all fruitflies.

Thus, *Cyrtophora* species attacked flies predominantly by biting, even when flies equalled or exceeded the weight of the spider (as in the case of blowflies given to C. *monulfi*). Wasp-mimicking stratiomyid flies (soldier flies), however, elicited 66.7 percent wrap-restraints is *C. moluccensis*. As *C. moluccensis* attacks most hymenopterans by wrapping (based on incidental observations), it is suggested that the spiders mistook the stratiomyids for wasps and treated them accordingly. There is some evidence to support this: more than half of the wrap attacks were of type 1 (wrap/bite), in which the wrap was of short duration (2 to 17 seconds), and was followed by a long bite not significantly different in duration from the bite given in a bite/wrap attack sequence. One may postulate that the spider switches off the wrap attack as soon as it recognizes the prey to be non-hymenopterous. Recognition may occur only upon actual contact with the prey, after immobilization wrapping has begun. Since prey discrimination in orb-weavers is based on tactile and chemosensory cues, the wasp mimicry of stratiomyids must extend to non-visual characters, e.g. wingbeat frequency, for the spider to err in their recognition.

Argiope argentata attacked 74 percent of live blowflies and 98 percent of live stingless bees (*Trigona* sp.) by wrapping (Robinson and Olazarri, 1971). However, Peters (1931, 1933) found that vibrating blowflies were bitten by *Araneus diadematus*, and *Eriophora fuliginea* attacked most stingless bees by biting and pulling out (Robinson *et al.*, 1972). The latter authors suggested that a biting attack is elicited by small, rapidly vibrating prey that have become trapped by only a few viscid spiral elements and may, therefore, easily escape. Since *E. fuliginea* has a coarser mesh web than *A. argentata*, stingless bees are held by fewer threads (often only one), this may explain the predominance of biting attacks in *E. fuliginea*. Because of its non-adhesiveness, the *Cyrtophora* web is relatively inefficient in restraining small, active insects (see evidence on blowfly escapes from *C. moluccensis* webs, Chapter 2), hence, a rapid biting attack would be most effective.

Transportation sequences with flies are variable (see Tables 15 to 18). Blowflies are carried entirely on silk by *C. monulfi* and predominantly on silk by *C. citricola* (95 percent) and *C. cylindroides* (59.1 percent). *Cyrtophora moluccensis* uses both methods with equal frequency. Stratiomyids, which are heavier than blowflies, are carried mainly on silk. Fruitflies, which are small and light, and are not wrapped at the capture site, are carried in the jaws by *C. citricola*.

When fruitflies were tested in rapid succession, *C. citricola* attacked each additional fly while retaining the previous ones in the jaws, thus accumulating up to 5 fruitflies in the jaws. However, after 4 to 5 fruitflies had been accumulated, they were wrapped together into one prey package, and transferred to the spinnerets. Four to 5 fruitflies weigh approximately 40 to 50 mg, and are within the weight range of blowflies which are carried on silk by *C. citricola*. These observations imply that prey weight dictates the mode of transportation to the hub in *Cyrtophora*, though other factors such as size and bulkiness of the prey may also be important.

Sequences with Orthopterans

Orthopterans may be immobilized either by biting or by wrapping. Although wrap restraints (sequences 1 and 2) occur more frequently in *C. moluccensis* and *C. citricola*, no one sequence predominates in all four species. The significant fact is that three attack sequences, involving both wrap and bite immobilization, are commonly used on one type of prey.

Argiope argentata wraps all crickets (Robinson and Olazarri, 1971). Other *Argiope* species also wrap most orthopterans (Robinson, personal communication). These authors have suggested that wrapping enables the spider to restrain dangerous prey while maintaining a safe distance from it. Species that do not attack prey by wrapping (e.g., *Nephila clavipes*), often restrain orthopterans and other large prey with a repeated bite/back-off sequence that is considerably less efficient than a wrap immobilization (Robinson *et al.*, 1969).

Since immobilization wrapping does occur in *Cyrtophora* species, why is it not used more frequently with orthopteran prey? Perhaps, because of the strength and density of the horizontal orb-web, *Cyrtophora* is more protected from potentially dangerous prey than is *Argiope* (or any other typical orb-web spider). The horizontal net is always situated between the spider and its prey. Hence, the spider can "afford" to utilize a more direct bite immobilization rather than wrapping from a distance. An analogy may be drawn between the methods of attack of *Cyrtophora* species and that of the sheetweb spider (Linyphiidae) or purse-web spider (Atypidae), both of which seize their prey in the jaws from a position of relative safety beneath a layer of silk. Furthermore, since the horizontal net forms a barrier between the spider and its prey, it is difficult for *Cyrtophora* to completely immobilize prey by wrapping unless a large portion of the insect protrudes through the net into the thread-free zone. Katydids are often not heavy enough or strong enough to break the net of a *Cyrtophora* web, and in such instances direct immobilization by biting may be more effective. Orthopterans that struggle and damage the net may be immobilized entirely by wrapping. Many of the wrap/bite sequences given to orthopteran prey consist of a short duration wrap and long duration bite, as already observed with stratiomyid flies. As with stratiomyids, it is possible that the initial wrap attack is switched off upon some sort of feedback from the prey, e.g. prey harmless, or prey body not protruding through net. The predominance of biting attacks on blowflies may also be explained in this manner. Although sample sizes are too small to be conclusive, both *C. moluccensis* and *C. cylindroides* attacked more insects in the barrier web by wrapping (9 out of 14) than by biting. As there is no net separating the spider from its prey in the upper barrier web, a wrapping attack may be both safer and more efficient.

Predatory sequences initiated by immobilization wrapping in *A. argentata* were shorter than those initiated by biting (Robinson, *et al.*, 1969). It was suggested that another advantage to the spider of restraint wrapping was to minimize time spent away from the hub, the hub offering both protection and a central location for monitoring web vibrations. This seems particularly applicable to *Argiope* which returns to the hub after immobilization wrapping, leaving the prey in the web. *Cyrtophora* does not leave wrapped prey in the web, and although sequences in which prey are restrained by wrapping alone (sequence 2) are somewhat shorter in duration than sequences initiated by either bite/wrap or wrap/bite attacks, the reduction in time spent away from the hub is not so pronounced as in *A. argentata*. Thus, the advantages of a wrapping attack may be more limited for *Cyrtophora* species.

Orthopterans were invariably carried to the hub on silk, though crickets of the same or greater weight than the orthopterans were carried in the jaws by *A. argentata* (Robinson, 1969, *A. argentata* weighs approximately the same as *C. moluccensis*). It may be more difficult to carry heavy prey in the jaws under a horizontal orb-web than under a near-vertical web. In the case of a horizontal orb, the spider exerts a force normal to the web equal to its entire body weight, but if the web is tilted, only a small component of the spider's weight acts normal to the web. This implies that, with equal weight spiders, the free space between the spider's body and the web surface would be less given a horizontal web than given a tilted web. Thus, *Cyrtophora* may have less space to carry large or bulky prey in the jaws and must resort to carrying them on silk. This hypothesis remains to be tested.

Sequences with Dragonflies

The dragonflies tested on *C. moluccensis* weighed approximately the same as the katydids, and the observed predatory sequences were similar to those with katydids as prey, i.e., wrapping attacks (sequences 1 and 2) and biting attacks (sequence 3) occurred with almost equal frequency. The hypothesis proposed to explain the occurrence of all three sequences with orthoptera prey may be applied to dragonflies as well.

Dragonflies are given a much longer bite, whether it be an immobilization or post-immobilization bite, than are katydids. Thus, bite duration does not appear to be weight dependent, but may be related to other factors such as intensity of struggling of the prey or prey shape.

Dragonflies, like grasshoppers and katydids, are carried to the hub on silk.

Sequences with Beetles

Small weevils (ca. 35 mg) and large scarabid beetles (500 to 1000 mg) were tested on *C. moluccensis*. All beetles were immobilized by wrapping. Attack sequence 2, wrap/cut out/free wrap, was used on most weevils. About 30 percent, however, were given short, exploratory bites after the initial wrapping restraint. Half of these were carried to the hub in the jaws, and half were wrapped again and transferred to the spinnerets. This method of attack seems to be a variation on the typical wrap/bite sequence, where a series of short test-bites replace the long bite normally given to non-coleopteran prey.

The attack sequence with large scarabs (*Melolontha* sp.) is a more complex variation of sequence 1, involving the behaviors wrap/attach thread to net (or hub)/test-bites/wrap, which may be repeated several times. A typical attack sequence on *Melolontha*, taken from field notes, is as follows:

> Spider on hub. Under net, to prey in web. Touch and palpate. Wrap (throw silk swathes under prey). Cut out with jaws while wrapping. Attach thread to net. Wrap (move over surface of prey). Begin rotating prey while wrapping (rotate-wrap). Test-bites. Rotate-wrap. Attach thread to net near hub. Test-bites. Rotate-wrap. Attach thread to net. Test-bites.

Rotate-wrap Cut proximal thread to net and attach thread closer to hub. Turn 180° at hub. Pull prey up with legs I and II. Manipulate with legs I and II, jaws and palps.

The hard and smooth exoskeleton of most coleopterans precludes rapid immobilization by biting. Some beetles also have an oily coating on the exoskeleton which may enable them to slip through spider webs. Small beetles, such as the weevils tested on *C. moluccensis*, would slip through the horizontal net unless immediately wrapped by the spider. Large *Melolontha* sp. were both active and heavy enough to break through the horizontal net, and also escaped unless wrapped immediately. Beetles were also observed to slip through the enswathing silk. This may explain the necessity for the long duration, repeated wrapping bouts that are given to *Melolontha* sp. Both weevils and scarabs were wrapped repeatedly at the hub during manipulation and early stages of feeding.

Beetles were never attacked by a simple wrap/bite sequence. Although experiments testing the importance of various cues have not been performed, perhaps penetration through a beetle's armour is difficult and a large number of short, exploratory bites are necessary before the spider can select a spot through which the venom and digestive enzymes can be injected. It is doubtful whether a great deal of venom can be injected in the duration of a test-bite. As a result, complete immobilization of the prey is slow and beetles must be wrapped repeatedly to avoid loss.

Both *Eriophora fuliginea* and *Argiope argentata* attacked *Tenebrio* beetles (about 1/4 the size of *Melolontha* sp.) with a repeated wrap/bite sequence, similar to that used by *G. moluccensis* on scarabs (Robinson and Olazarri, 1971, Robinson, *et al*., 1972). Robinson and Robinson (unpublished) tested *Melolontha* sp. on *Nephila maculata* and on *Argiope aemula* in New Guinea and found that although both responded with lengthy, complex sequences, *A. aemula* dealt more efficiently with the beetles than did the larger *N. maculata*. The latter lacks the wrap immobilization behavior, and attacks large prey by a repeated bite-and-back-off sequence. Thus, the wrapping attack, even when prolonged, is more effective with hard-cuticled prey such as beetles.

In 6 out of 13 complete predatory sequences, *Melolontha* were carried to the hub on silk. In the remaining instances, a sharply defined carry stage did not occur, rather, with each wrap/attach thread sequence, the prey was moved slightly closer to the hub. This method of transporting prey to the hub occurs frequently in several species of *Gasteracantha* and *Micrathena* with prey that are too heavy (or bulky?) to be carried in the jaws. These species do not carry prey on silk. Probably carry-on-silk behavior evolved from this simpler but less efficient behavior of wrap/attach thread to hub. The large scarabs tested on *G. moluccensis* may have been near or at the upper weight limit of prey that can be carried on silk. A 1 g scarab will exert a force of approximately 1 x 10^3 dynes on the carrying thread. Assuming that the silk used by *G. moluccensis* for wrapping and transporting prey is similar in physical properties to the web silk, the carrying thread would break under a force of approximately 3 x 10^3 dynes (see Chapter 2), three times the force exerted by the beetle. Most likely, carry-on-silk behavior is replaced by the wrap/attach thread to hub sequence at prey weights well below those that would exert a breaking force on the silk.

Sequences with Pentatomids

Pentatomids (stink-bugs) were tested on *C. cylindroides*. Ninety percent were attacked by wrapping (sequence 2). The remaining 10 percent were given short test-bites (too short to measure accurately), and were then treated like the rest. Pentatomids are well known to discharge copious defense secretions. It has been suggested that spiders that immobilize prey by wrapping can attack pentatomids and other hemipterans with greater efficiency than can species with only bite immobilization behavior, as they can avoid the main force of the discharge (Robinson and Olazarri, 1971). Twelve (60 percent) of the twenty pentatomids tested were actually observed to discharge upon being attacked by the spider, and the others may have discharged as well, as inferred from the behavior of the spider.

In 60 percent of the sequences with pentatomids, spiders interrupted the attack, stopping to rest on or near the prey and clean the palps, legs and mouthparts. Spiders gave the appearance of being stunned by the discharge, remaining immobile for durations of a few seconds to over five minutes, before initiating cleaning or resuming the attack. During this time, the pentatomid could free itself from the web and escape. Many attacks on pentatomids by *C. cylindroides* were unsuccessful. Nonetheless, remains of pentatomids and of other hemipterans were found in prey traps under *C. moluccensis* webs, indicating that this species, at least, does trap pentatomids under natural conditions (Lubin, in preparation).

Pentatomids, though lighter than blowflies, were always carried on silk. This is undoubtedly due to the noxious secretions. It is unclear how long it takes for the secretion to become exhausted. Pentatomids were transported in the jaws by *A. argentata* (Robinson and Olazarri, 1971); however, this may have been after a period of resting at the hub, during which the secretion had dispersed. In most instances, *C. moluccensis* did not begin to feed immediately after suspending a pentatomid at the hub, but remained resting at the hub or began cleaning. In general, predatory sequences with pentatomids were more likely to be interrupted by resting or grooming behavior at any stage from the initial attack to final manipulation at the hub, than sequences with any other prey tested. In some cases, interrupted sequences could be specifically related to discharge of noxious secretion by the prey.

Sequences with Multiple Prey

Insects given to spiders that already have prey at the hub are treated as first prey. Second or third prey are not left in the web, but given a complete predatory sequence. This was determined by presenting multiple prey (fruitflies, blowflies and katydids) to *C. citricola*, *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Many other species, including *A. argentata* and *Gasteracantha* species leave second or third prey wrapped in the web, and return to feed on the first prey at the hub. Except in the case of very small fruitflies given to *C. citricola* in rapid succession (see p. 89), each successive prey is treated separately. All prey are suspended individually near the hub and the order in which they are eaten is not necessarily the same as that in which they were suspended. If the spider is already feeding on an insect at the hub, it will usually resume feeding on it after returning from further captures.

By suspending all prey at the hub, *Cyrtophora* may spend more time in prey capture and transportation than species that leave multiple prey in the web; on the other hand, it may also lose fewer prey to inquilines, since prey at the hub can be easily defended.

Discussion

Similarities between predatory behavior units of *Cyrtophora* spp., *A. argentata* and *E. fuliginea* have been noted throughout the text. A summary of units of predatory behavior and their presence or absence in *Cyrtophora* and *Argiope* is given in Table 19. Behaviors that were not observed in *Cyrtophora* but that occur in *A. argentata* are maintenance of dragline connection with the hub, resting at the hub during a prey capture sequence, and "Rundgang" behavior (Peters, 1931), involving multiple attachment of wrapped prey to the hub by dabbing the spinnerets against the hub as the spider turns in an arc of 180°. Web shaking is the only behavior observed in *Cyrtophora* that does not seem to have a functional counterpart in *A. argentata* or in *E. fuliginea*.

Attack sequences of *Cyrtophora* and *Argiope* with different prey types are compared and summarized in Table 20. Differences in the attack sequences with flies (other than stratiomyids), orthopterans, and dragonflies as prey have already been noted. The wrap/short bite sequence, which *Argiope* uses with most prey other than moths, is less

Table 19. Summary of predatory behavior units of *Cyrtophora* and *Argiope*. Data on *A. argentata* from Robinson and Olazarri, 1971.

Behavior	*Cyrtophora*	*Argiope*
Dragline to hub	-	+
Plucking, tensioning	+	+
Web shaking	+	-
Bite immobilization	+	+
Wrap immobilization	+	+
Rest on prey	infrequent	+
Rest at hub	-	+
Pull out	+	+
Cut Out	+	+
Carry in jaws	+	+
Carry on silk	+	+
Wrap at hub	+	+
Randgang	-	+

Table 20. Summary of behavior sequences *Cyrtophora* and *Argiope* with different prey types. Only predominant initial attack sequences are shown. Data on *A. argentata* are from Robinson and Olazarri, 1971

Prey	*Cyrtophora*	*Argiope*
Moths	bite/wrap	long bite/wrap
Blowflies	bite/wrap bite/pull out	wrap/short bite bite/pull out
Orthopterans	wrap/bite wrap bite/wrap	wrap/short bite
Dragonflies	wrap/bite wrap bite/wrap	wrap/short bite
Beetles	wrap wrap/short bites	wrap/short bites
Pentatomids	wrap	wrap/short bite

clearly defined in *Cyrtophora*, and a broader spectrum of prey types may be immobilized by biting. Immobilization wrapping may have certain disadvantages for *Cyrtophora* due to peculiarities of the non-sticky, knockdown web (p. 90).

The similarity of prey capture behaviors of *Argiope* and *Cyrtophora* is initially quite astonishing, considering the differences in the basic trapping strategies of their webs. In the previous chapter, a hypothesis was presented as the nature of the selective forces that may have brought about the evolution of a *Cyrtophora*-type web. These were mainly environmental factors such as rain and wind, and prey availability in open habitats. The evolution of a new trapping strategy, along with drastic modification of web structure, appear to have changed the predatory behavior of *Cyrtophora* only slightly. I suggest that *Cyrtophora* diverged from an *Argiope* or *Araneus*-like precursor, in which complex predatory behavior including both wrapping and biting repertoire already existed, and that only small changes in predatory behavior were necessary to comply with the new web type. These changes were:

1) Loss of a dragline connecting with the hub during prey capture activities. As the *Cyrtophora* web is persistent, an accumulation of draglines on the horizontal orb would probably interfere with signal transmission to the hub. This would reduce the trapping efficiency of the spider and would therefore be strongly selected against.

The dragline, considered by many a primitive form of silk production (Kaston, 1964, Savory, 1952), is found in all other orb-web spiders. *Cyrtophora* species (and probably also the related New World genus

Mecynogea) have evolved an ability to switch off dragline production during locomotion under the net. Other orb-web species use the dragline for rapid return to the web, either by climbing up the thread (e.g., *Nephila*, in a "head-over-foot" motion) or by swinging out on it (e.g., *Leucauge*), for dropping out of the web when disturbed, and for hanging from the web surface during prey capture. In all of these activities, *Cyrtophora* dispenses with the use of a dragline. The lower barrier web of *Cyrtophora* would probably interfere with the spider swinging out on a dragline, and I can see no advantage to walking on a dragline under a horizontal, non-sticky web, over walking on the web itself. Furthermore, when disturbed, *Cyrtophora* does not normally drop out of the web, but climbs into the barrier web or nearby vegetation. A similar escape behavior was observed in *Mecynogea* (Exline, 1948). (The exception is *C. cylindroides* which, upon repeated disturbance, hurls itself out of the web without a dragline. This will be described in another paper). During prey capture, *Cyrtophora* hangs from the web or from the prey by legs I and II (during wrapping) or by legs IV (during biting). As the *Cyrtophora* web is uniformly strong and fine-meshed, supports are more readily available than in a typical orb-web with its weak viscid spiral (in many instances, the viscid spiral alone could not support the weight of the orb-weaver, see Chapter 2). Based on these considerations, I suggest that the loss of dragline production in *Cyrtophora* during locomotion on the web came about with the evolution of the non-adhesive, knockdown web.

2) Reduction in the use of wrapping for prey immobilization. The wrap attack is restricted more to beetles, pentatomids and hymenopterans,

as well as some large insects of other types that can break through the horizontal net. As noted above, the horizontal net acts as a barrier between the spider and its prey, making it safer to attack prey directly by biting and, at the same time, more difficult to restrain most insects solely by wrapping. A wrap immobilization may be more effective with prey caught in the upper barrier web; sample sizes, however, are insufficient to verify this.

3) Loss of the behavior involved in leaving wrapped prey at the capture site and resting on the hub during the prey capture sequence. Dead or motionless insects in the web are generally not detected by *Cyrtophora*. During nocturnal web repairs, *Cyrtophora* may retrieve some of these, on several occasions however, *C. moluccensis* was observed to reject dead insects. It is possible that with the diffuse signal transmission through the net (see Chapter 2), *Cyrtophora* is unable to detect and locate motionless objects in the web. Under such circumstances, there would be selection against leaving immobilized prey in the web.

4) Loss of "Rundgang" behavior. As the function of this behavior is not known precisely, it is difficult to speculate on reasons for its loss. Possibly, since *Cyrtophora* has a horizontal net, there is no need to distribute prey weight evenly around the hub, or *Cyrtophora* threads may be sufficiently strong, so that multiple attachments to the hub are unnecessary. Robinson *et al.* (1972) suggested that an open hub (e.g., that of *Eriophora* or *Araneus*) is weaker than a closed hub (e.g., that of *Argiope*) and, therefore, a more even distribution of prey weight is necessary. *Cyrtophora* webs have an

open hub, but it is irregular in shape and the fine-meshed web around the hub lends stronger, cross-braced support for suspending prey packages.

Kaston (1964) and Kullmann (1958, 1972) suggested *Cyrtophora* as a link between the sheetweb-building Linyphiidae and the Araneidae. Earlier, McCook (1889) suggested that the related New World genus *Mecynogea* (the Basilica spider) was similar to the Linyphiidae in its manner of web construction. Kaston (1964) placed *Cyrtophora* (and *Mecynogea*) between the linyphiids and the genus *Nephila* in his scheme of the evolution of spider webs, based on the following similarities:

1. *Cyrtophora*, like the linyphiids, constructs a non-adhesive, three-dimensional, knockdown web.
2. Both *Cyrtophora* and *Nephila* have irregular barrier webs on either side of the orb.
3. *Cyrtophora* and *Nephila* webs have bifurcated radii toward the periphery of the orb and retain the non-adhesive, structural spiral (*Nephila* webs have a viscid spiral as well).

The linyphiid web consists of an irregularly constructed horizontal sheet with a barrier web above and below it. The irregular sheet, which may be domed or tent-shaped (as in the web of *Linyphia marginata*), lacks the basic elements of an orb-web: the radii, spiral and hub. It is difficult to imagine the complex orb-web of *Cyrtophora* derived from the unstructured sheetweb of a linyphiid. Hence, structural similarities between *Cyrtophora* webs and those of linyphiids are probably superficial ones, resulting from convergent evolution. Exline (1948) arrived at the same conclusion regarding *Mecynogea*, based both on web structure and on spider morphology. The implied relationship between *Cyrtophora* and *Nephila* is equally tenuous. The barrier webs of *Cyrtophora* and *Nephila* have probably evolved independently (Robinson and Robinson, unpublished, discuss the evolution of the barrier web in *N. maculata*). Forked radii occur in webs of several araneids, including *Z. fuliginea*, and are, therefore, not unique to *Nephila* and *Cyrtophora*. They may be characteristic of large orb-webs. without forked radii, mesh size toward the periphery of the orb would become too large. Finally, on the basis of predatory behavior analyses, I contend that *Cyrtophora* is quite removed from both the linyphiids and the genus *Nephila*. *Cyrtophora* predatory behavior is similar to that of *Argiope*, *Araneus*, and *Eriophora*, and includes the advanced element of immobilization wrapping. Prey immobilization by wrapping does not occur in linyphiids (Bristowe, 1941) or in *Nephila* (Robinson, *et al.*, 1969, Robinson and Mirick, 1971). On this evidence alone, it is unlikely that *Cyrtophora* separated from the main line of araneid evolution prior to the evolution of restraint wrapping. The differences between the predatory behaviors of *Cyrtophora* and *Argiope* clearly involve a reduction of certain behavior elements concomitant with the evolution of a specialized web.

Summary

1. Units of predatory behavior described in four species of *Cyrtophora* include resting positions, plucking, web shaking, prey immobilization, cutting and pulling out, transportation to the hub and manipulation at the hub. With the exception of web shaking behavior, all units

of behavior are similar to those of *Argiope argentata*.

2. Four major behavior sequences with various prey types are recognized and compared with predatory behavior sequences of other araneids, especially *A. argentata*.

3. The predatory behavior of *Cyrtophora* differs from that of *Argiope* in the following aspects:
    - a) loss of dragline connection to the hub
    - b) restriction of immobilization wrapping
    - c) loss of behavior of leaving prey in the web and resting at the hub
    - d) loss of Rundgang behavior

4. I suggest that *Cyrtophora* evolved from an *Argiope*-like araneid in which advanced predatory behavior already existed.

CHAPTER 4. COMMUNAL BEHAVIOR AND POPULATION DYNAMICS OF *CYRTOPHORA MOLUCCENSIS*

Introduction

The orb-web spiders *Cyrtophora moluccensis* and *C. citricola* are found predominantly in dense colonies. Wheeler (1926) appears to be the first to mention the gregarious habits of *C. citricola*. (Darwin, in *The Voyage of the Beagle*, commented on aggregations of a large orb-web spider in South America which Shear (1970) interpreted to be *Cyrtophora*, Darwin noted, however, that the orb-webs were vertical and as *Cyrtophora* webs are always horizontal, he was most likely observing an aggregation of *Nephila* sp.). Wheeler observed that in *C. citricola* colonies in the Canary Islands "individuals of all ages live together amicably and seem to feed in common on the prey that is caught in the webs." Darchen (1965), however, noted competition for prey between individuals within *C. citricola* colonies.

Recent reviews of social organization in spiders (Kullmann, 1968, 1970-71, Shear, 1970; Wilson, 1971) generally agree that *C. citricola* exhibits a low level of sociality, characterized by persistent aggregation of members of all age groups with possibly some form of cooperation between colony members. This is "communal organization" in Michener's (1969) classification of levels of insect sociality (adopted by Wilson, 1971). A similar situation is inferred in *C. moluccensis*. The precise level of sociality of *Cyrtophora* colonies, however, remained to be investigated.

The basic questions still facing students of social behavior are: what are the adaptive advantages of social organization, and how did sociality evolve? The problems are most readily approached by examining organisms at lower levels of social organization and, particularly, by comparing them with their nearest asocial relatives. This approach has proven fruitful, for example, in studying the development of brood care in crickets (Alexander, 1961), and the evolution of social behavior in bees (Michener, 1969) and in wasps (Wheeler, 1923, Evans, 1958). Kaston (1965) suggested that the levels of social organization in theridiid spiders might be explained in terms of increasing parent-offspring interactions.

Observations on five species of *Cyrtophora* in the vicinity of Wau, New Guinea (Morobe District) led me to believe that useful comparisons could be drawn between levels of social organization in these species. Of the five species of *Cyrtophora*, only *C. moluccensis* exhibited a communal level of sociality. This species was, therefore, studied in detail and comparisons were made with less social species whenever possible.

Distribution of *Cyrtophora* Species in Wau

Five species of *Cyrtophora* were observed in the Wau area. *Cyrtophora moluccensis*, the largest (♀ 20 to 25 mm) and the only communal species observed, is found in open, disturbed habitats. Table 21 lists the locations of some colonies in the Wau area. They were characteristically in tall trees, most frequently pine or araucaria, (Figure 11), or in other elevated situations. The individual web, as described in Chapter 2, is composed of a horizontal, fine-meshed orb-web with an irregular

Table 21. Distribution of C. melaccensis colonies in the vicinity of Wau, New Guinea.

	No. Colonies Observed	Habitat	Approx. hgt. Above Ground
1. Colonies with ≥ 10 members	9	*Araucaria* spp.	2 to 10 m
	5	*Pinus* spp.	2 to 10 m
	2	Edge of coffee plantations	2 to 4 m
	6	Unidentified trees, shrubs, and tall grass	up to 10 m
	3	Telephone or electricity wires	up to 8 m
Total	25		
2. Groups with < 10 members, and solitary individuals		Abandoned citrus grove	2 to 5 m
		Araucaria hunsteinii and *A. cunninghamii* plantations	> 3 m
		"Kunai" grass and roadside vegetation	< 3 m

Figure 11. A colony of C. _moluccensis_ (colony 1) in a pine-tree.

barrier web above and below. In the colony, adjacent webs are interconnected via their barrier webs, so that the overall impression is one of "a very irregular structure or framework....and a variable number of suborbicular, horizontal webs, suspended side by side or one above the other in the framework" (Wheeler, 1926, on the structure of *C. citricola* colonies). Colonies often span gaps between adjacent trees or other supports. Small aggregations and solitary *C. moluccensis* are less common, many of these may be newly established colonies.

Cyrtophora monulfi (♀: 8 to 10 mm) inhabits tall grass in open meadows, roadside vegetation and low shrubs. Webs are rarely over 3 m above ground level. Loose aggregations of *C. monulfi* webs, in which individuals share some structural threads of their barrier webs, are found along fences or hedges bordering grassy fields.

The remaining three species are entirely solitary. *Cyrtophora cylindroides* (♀: 15 mm) is a brightly colored species found in second-growth rainforest and mature *Araucaria* stands. Solitary webs are located high in the branches. In two locations where small aggregations and solitary *C. moluccensis* were found in *Araucaria* stands together with *C. cylindroides*, the latter occupied shadier spots adjacent to the tree trunks, while the former occupied the more exposed, peripheral areas. In the Wau-Bulolo area *C. cylindroides* is considerably rarer and patchier in distribution than *C. moluccensis*, or the grassland species *C. monulfi* and *C. cicatrosa*.

Cyrtophora cicatrosa (♀: 6 to 7 mm) and an as yet unidentified species (species "D"; ♀: 4 to 5 mm) are predominantly open grassland and forest clearing dwellers. Webs of *C. cicatrosa* are also found in araucaria and pine trees, mainly in exposed locations near the tips of branches. Species "D" is cryptically colored and relatively uncommon. Webs are located near the ground in tall grass, and also in low vegetation along forest edge and in forest clearings. Little is known of the behavior of this species.

Materials and Methods

Two *C. moluccensis* colonies were observed for a total period of 85 hours during four time intervals (0800-0900, 1200-1300, 1600-1700, and 2000-2100). Both colonies were located in pine trees on the grounds of the Wau Ecology Institute. Colony 1, containing approximately 75 individuals, was observed during the period of May 19th to July 6th, 1971, colony 3, with approximately 30 members, was observed during the period of November 16th to December 12th, 1971. The observer sat on a perch 3 to 4 m from the edge of the colony and approximately 3 m above the base of the colony. Nocturnal observations were made with the aid of a headlamp. By using the light briefly and rapidly scanning the colony every few minutes, the chances of disturbing the spiders or attracting large numbers of insects to the colony were minimized.

Interactions between colony members were observed in colony 3 and the numbers of interactions of each type were recorded (40 hours observation). Also recorded were the total number of insects flying into colonies 1 and 3, the number of actual captures and insect escapes, and the number of insects that actively avoided the colonies. Insects were identified to order whenever possible. Butterflies, moths, large beetles, wasps and some flies could be readily identified from a distance, many other insects were recognized by their characteristic flight patterns. Avoidance of colonies by flying insects was recorded only during the day. Visits of an unidentified dipteran (sarcophagid) egg-case parasite were noted and the interactions between colony members and the parasite were described.

Other data on egg-case production, parasitism and protection of egg-cases were obtained from observations of *C. moluccensis*, *C. monulfi*, *C. cylindroides* and *C. cicatrosa*. The egg-cases of all these species are suspended above the hub in chronological order. In *C. moluccensis*, *C. cylindroides*, and *C. cicatrosa* the most recent egg-case is the lowest one in the string, in *C. monulfi* the order is reversed, the most recent one being the one closest to the mouth of the retreat.

Four *C. moluccensis* colonies were censused weekly. These censuses and data on formation and growth of three experimental colonies near the field station were used to elucidate the population dynamics of *C. moluccensis* colonies. The longevity of adult *C. moluccensis* was determined from small groups located in a citrus plantation, by measuring or estimating intervals between consecutive egg-case productions, and the interval between the last egg-case produced and death, an estimate was obtained of the life span of the spider.

Interactions Within *C. moluccensis* Colonies

There is no evidence for active cooperation between individuals in *C. moluccensis* colonies. Each member rests in an inverted position at the hub of its own orb-web, and each web within the colony is a complete, self-sufficient structure containing all the elements found in the solitary web. Prey capture, web renewal and repair and construction of egg-cases are all solitary activities. Aggressive interactions, however, occur between colony members during prey capture activities and during web repair and renewal (Table 22). These interactions were observed frequently enough to be considered part of the "normal" behavioral repertoire of communal *C. moluccensis*. As intraspecific interactions between asocial orb-web spiders are generally confined to mating behavior and occasional predation, interactions on any other level are likely to shed light on the nature and adaptive value of communal organization.

The predatory behavior of *C. moluccensis*, *C. citricola*, *C. monulfi* and *C. cylindroides*, as described in Chapter 3, is essentially the same in all species. The upper barrier web acts as a knockdown device for flying insects. Insects striking the barrier web may fall onto the horizontal net (orb-web) and are restrained to some degree by the dense snare above the net and by the resiliency of the non-sticky, fine-meshed net. *Cyrtophora* attacks insects from under the horizontal net or by climbing into the upper barrier web. Insects are rarely attacked in the lower barrier web. Aggressive interactions over prey were observed most often with large, active prey, or with rapidly vibrating prey caught in the upper barrier web or in the irregular structural threads at the periphery of the horizontal net. One such aggressive interaction occurred as follows:

> A katydid in the upper barrier web of ♀1 was attacked by wrapping by ♀1. A larger spider, ♀2, entered the barrier web from above and began wrapping the katydid (after touching it with legs I). ♀1 plucked the barrier web near the

Table 22. Aggressive interactions between C. *moluccensis* adults and subadults in a colony during prey capture and web renewal and repair, expressed as percentages of total interactions during 10 hours of observation in each of 4 time intervals (0800-0900, 1200-1300, 1600-1700, 2000-2100).

	No. Interactions	Percent of Total Interactions			
		0800-0900	1200-1300	1600-1700	2000-2100
Prey Capture	14	28.6	---	35.7	35.7
Web Repair and Renewal	108	---	---	---	100
Total	122	3.3	---	4.1	92.6

prey. ♀ 2 plucked the barrier web and continued wrapping. ♀ 1 ran down to the edge of the horizontal net and remained there while ♀ 2 wrapped the katydid, cut it out and transported it on silk to her own web.

Web renewal and web repair were described in Chapter 2. The horizontal net is completely rebuilt only once every 2 1/2 weeks on the average. Nightly repairs of the horizontal net are minimal; however, spiders were often observed climbing through the barrier web, plucking and tensioning the threads and laying down additional ones. At any one moment during observations between the hours of 8 to 9 P.M., up to 20 percent of the spiders could be seen away from the hub, apparently occupied in web repairs. Since observations were not continued throughout the night, the total duration of these activities is not known.

Spiders active in examining and repairing the barrier webs wandered far outside the limits of their own webs. Individuals from the center of a colony were seen adding structural threads to supporting branches on the periphery of the colony. To do this, they may have traversed 4 to 6 conspecific webs and interacted with at least that number of spiders. Five levels of aggression were distinguished in the behavior of the defender towards an intruder.

1. Tensioning: the defending spider, resting at the hub, turns toward the intruder and pulls the horizontal net toward with legs I and II.
2. Plucking: as above, but the motion is a sharp, jerking one.
3. Web shaking: the net is shaken in a rapid, vertical motion with legs I and II.

4. Running out and web shaking: as above (No. 3), but the spider leaves the hub and runs toward the intruder, pausing frequently to shake the mat.
5. Fighting: as fighting was observed on only three occasions and in each case lasted only a few seconds, no accurate description is not possible. Contestants approached each other face-to-face and appeared to tap each other with legs I and II while bouncing up and down under the net.

All of the above behaviors, with the exception of fighting, occur in response to any web disturbance and constitute a normal part of prey capture behavior (Chapter 3).

Although critical distances between intruders and defenders were not measured, it was apparent that as the intruder neared the hub of the defender, increasingly aggressive interactions occurred. Only three of the 108 interactions during web repair resulted in the intruder displacing the defender, and in all three instances the intruder was the larger individual. One of these seemed to be a permanent displacement, the other 2 intruders left after several seconds and the original occupants returned to their webs. Observations on an experimental colony (see later) suggest that web-capture and occupation of abandoned webs, either temporarily or permanently, are not uncommon phenomena in *C. moluccensis* colonies. The function of this behavior remains unknown and the problem deserves further attention.

Although interactions between colony members occur regularly, especially during nocturnal web repairs these interactions did not usually result in injury or death. Immature *C. moluccensis* less than

8 mm in length were tolerated by adults, and their webs were often found within the barrier web framework of adult webs. As small theridiid inquilines (*Argyrodes* spp.) are also tolerated to some extent, as well as small *C. moluccensis* males (4 to 5 mm long), a critical size limitation may be involved. One cannot, however, rule out recognition of immatures (and males?) by other means. Tretzel (1961), for example, showed that the agelenid *Coelotes terrestris* distinguished its young from prey by their characteristic web vibration frequency.

Cannibalism, though rare, occurred in several circumstances:

1. Remains of male *C. moluccensis* were found under webs of adult females on five occasions, and one such act of cannibalism was observed during attempted courtship. *Cyrtophora moluccensis* females probably mate only once and there appears to be a definite period of 4 to 7 days during which males are attracted to the female. [Sperm storage seems to be widespread in spiders (Bristowe, 1958) and is well documented for theridiid, *Achaearanea tepidariorum* (Valerio, 1970) and for *Cyrtophora cylindroides* (Lubin, in preparation).] Up to 12 males at a time were observed in the web of one female. Courtship and mating in *C. citricola* were described by Gerhardt (1928) and Kullmann (1964) and both authors commented that males were frequently eaten by females. Thus, no reduction in cannibalism during courtship is evident in the communal species of *Cyrtophora*

2. Newly emerged C. moluccensis immatures were seen feeding on fellow spiderlings in an experimental colony. This may be an unusual phenomenon caused by the restricted area. In nature, immatures begin to disperse as they build their first webs.
3. Four adult females were released near the house. The largest of these built a web over a period of two nights, and on two successive nights after the completion of her web, two of the remaining females were cannibalized. This is obviously unusual; however, a similar situation may occur when adults whose webs are destroyed by natural causes (e.g. falling branches) wander through the colony searching for a new web site. On one such occasion the wandering spider chased away a smaller individual and occupied its web.

I conclude that cannibalism is "normal" only in courtship and mating and that a lower level of aggressiveness is maintained in other interactions between colony members. Buskirk (personal communication) has shown that in the communal orb-web spider Metabus gravidus, the level of aggression is a function of the size of the interacting individuals and the distance between them. Since aggressive interactions occur during web building in this species too, it is likely that both here and in C. moluccensis such interactions serve to space individuals out within the colony and thereby optimize prey capture success for the individual. Such a spacing mechanism would obviously be under strong and continuous selective pressure. On this assumption, it is unlikely that increased cooperative or altruistic behaviors exhibited by the advanced social insects, could evolve in either *Cyrtophora* or *Metabus* colonies, as certain distances must be maintained between individuals to ensure an adequate food supply. An alternative would be fusion of webs to form one communal web, as in the social theridiid, *Anelosimus* sp., and the agelenid, *Agelena consociata*. This is considered an unlikely possibility in view of the structure and function of the orb-web.

Aggression during prey capture was also observed in loose aggregations of *C. monulfi*. Three such interactions were seen with prey presented to spiders during predatory behavior studies. The interactions were similar to those described in *C. moluccensis* but no fights were observed. It is not known whether aggression during web repair occurs in this species. As all other *Cyrtophora* species observed were solitary, there would be no occasion for interaction with conspecifics except during mating. The situation in *C. citricola* is believed to be similar to that in *C. moluccensis* (personal observations in West Africa and Kullmann, 1958).

Pros and Cons of Communal Organization

Disadvantages

Avoidance by prey

Cyrtophora moluccensis colonies are conspicuous to visually-orienting animals due to the dense, 3-dimensional structure of the individual webs as well as their exposed locations. The spiders themselves are conspicuous dark objects resting in the center of the horizontal orb. The egg-cones, which are greenish-white and suspended above the hub in the upper barrier web (Figures 7, 8 and 11) are also distinct, though it is often difficult to distinguish the spider itself from its string of egg-cases.

Colony conspicuousness has disadvantages. Many diurnal flying insects were observed to actively avoid *C. moluccensis* colonies by flying over or around them (Table 23). Some insect groups were more adept at colony avoidance than others, more than half the diurnal Lepidoptera (mainly butterflies) observed moving toward a colony succeeded in actively avoiding it. A large proportion of bees and wasps, and—in one colony—flies, also avoided the webs. Turnbull (1960) observed that butterflies and many of the higher Diptera and Hymenoptera were capable of both seeing and coordinating their flight to avoid the small, delicate webs of *Linyphia triangularis* (Linyphiidae). This has been corroborated by Robinson and Robinson (1970) in their studies of the prey of *Argiope argentata* (Araneidae) and by Bristowe (1941) in observations on several web-building spiders. Thus, it appears that the same types of flying insects that avoid spider webs in general, also avoid large colonies, and the chance of a flying insect failing to notice a colony may be considerably less. As colonies may persist for several years in one location, some long-lived insects may learn to consistently avoid them.

Lepidoptera, Hymenoptera, and Diptera combined comprised respectively 35 percent and 71.2 percent of the total number of insects observed flying toward colonies 1 and 3. In both series of observations, diurnal Lepidoptera were the largest single group of flying insects recorded, and yet throughout a period of one year, only two butterfly remains were retrieved from traps designed to catch prey remains from

Table 23. Active avoidance of two *C. moluccensis* colonies by flying insects. Row 1 is the total number of insects observed flying toward the colony. Row 2 is the percentage of insects of each order that actively avoided the colony.

		Lepidoptera	Hymenoptera	Diptera	Coleoptera	Other	Unidentified	Total
Colony 1 40 hours	No. Observed	217	62	71	14	5	408	777
	% Avoid	69.1	22.6	8.4	21.4	20.0	15.9	30.8
Colony 3 30 hours	No. Observed	524	78	133	23	26	249	1033
	% Avoid	59.0	47.4	42.8	13.0	30.8	20.9	45.1

these colonies (Lubin, in preparation). Evidently a large fraction of the potential prey, especially diurnal, visually orienting insects capable of accurate flight coordination, successfully avoid *C. moluccensis* colonies.

Predation and parasitism

The high-density of *C. moluccensis* individuals in a colony may also provide a conspicuous target for predators and parasites. This phenomenon has been documented in many instances, both in vertebrates and invertebrates, e.g. predation on schooling fish (Williams, 1966), parasitism in nesting colonies of birds (e.g., Smith, 1968), and numerous cases of specialized predation and parasitism in colonies of social insects (Wilson, 1971, reviews the recent literature on this subject). Predation on adult *C. moluccensis* by a spider-hunting wasp was observed only once, and then on a solitary adult. Spider-hunting wasps were seen on the periphery of *C. moluccensis* colonies, but nothing is known of their habits or degree of prey specificity. Two categories of parasites were found in the colonies:

1. Inquilines or kleptoparasites: mainly the theridiid spider, *Argyrodes argentatus* Cambr., but also unidentified hemipterans of the family Ploiariidae.
2. Dipteran and hymenopteran parasites of *C. moluccensis* egg-cases.

The nature of theridiid inquiline-host interactions in *C. citricola* webs was studied by Kullmann (1959) in a laboratory situation. *Conopistha argyrodes* (Theridiidae) was observed feeding on prey caught by *C. citricola*, either alongside the host or after cutting the thread by which the prey was suspended at the hub and removing it some distance away from the orb-web. Kullmann considered *Conopistha* to be an obligate parasite, so it did not build a web of its own and could not be kept isolated from the host web for any length of time.

In New Guinea, all webs of *C. moluccensis*, whether communal or solitary, harbored *Argyrodes* inquilines. On one occasion each, inquilines were observed feeding on newly emerged *C. moluccensis* young, on young inside the egg-case and on eggs through a small hole in the egg-case. I suspect that egg-cases that are damaged or parasitized by Hymenoptera or Diptera and rejected by the parent, may then be attacked by theridiid inquilines. Inquilines were always observed in the immediate vicinity of newly emerged *C. moluccensis* young. As the young remain aggregated and defenseless near the egg-case for 3 to 8 days after emergence, predation by theridiid inquilines may be a large source of mortality of young spiderlings. The question remains to be answered: are inquilines more abundant, and more destructive, in *C. moluccensis* colonies than in solitary webs? It has been suggested (Robinson, personal communication) that some orb-weavers, e.g. *Nephila clavipes*, *N. maculata* and *Argiope argentata*, may periodically relocate their webs in response to inquiline pressure. If this is the case, persistent *C. moluccensis* colonies may, indeed, face heavier inquiline infestations.

Parasites of *C. moluccensis* egg-cases included three species of *Baeus* (Hymenoptera Scelionidae) and an unidentified higher dipteran (Sarcophagidae). Larvae of the wasp and dipteran parasites fed on the eggs, pupated, and emerged through a hole in the egg-case. Parasitism did not necessarily destroy all of the eggs. The dipteran parasite was large enough to observe in action, and was remarkably adept at flying through *C. moluccensis* colonies without blundering into the barrier web threads. The fly picked its way through the webs, mainly by flying and hovering in the more open zones just beneath each horizontal net. Only webs with egg-cases were investigated closely by the fly.

Adult female *C. moluccensis* responded to the presence of the fly by violently shaking the horizontal net (Chapter 3) and by climbing up onto their egg-cases and encircling them with all four pairs of legs. This latter behavior was accompanied by an agitated waving of legs I, palpating and tapping the egg-case and plucking the barrier web threads around the egg-case. Web-shaking and directional response of *C. moluccensis* to parasite attacks occurred only while the fly was actually flying in or near the web. As soon as it landed in the barrier web or on an egg-case, the spider ceased to respond. This suggests that the spider responds to the wingbeat vibrations of the parasite (airborne or web-borne) which may be of characteristic frequency, but does not respond to low-level vibrations resulting from the parasite moving on the barrier web.

The numbers of dipteran parasite visits to two colonies at different times during the day are shown in Table 24. The percentage of successful attacks is not known. In many instances, the same fly returned to the colony again and again within a period of one hour. Parasite attacks were most intense during midday; this coincides with the time of day when many *C. moluccensis* females hang from the hub by

Table 24. Dipteran parasite visits to 2 colonies of *C. moluccensis* during 10 hours of observation in each of 4 time intervals (0800-0900, 1200-1300, 1600-1700, and 2000-2100).

	0800-0900	1200-1300	1600-1700	2000-21000	Total
Colony 1					
Total No. Visits in 10 hours	14	41	17	--	72
% of Total Visits	19.4	58.9	23.8	--	100
Colony 3					
Total No. Visits in 10 hours	9	18	2	--	29
% of Total Visits	31.0	82.1	6.9	--	100

legs IV in a characteristic sun-avoidance position (Chapter 3), and therefore, are in a position of minimal contact with both the web and the egg-cases.

Egg-cases from five colonies and from small aggregations in four areas were examined for evidence of parasitism (Table 25). The highest overall parasite counts occurred in the one old colony sampled (30.8 percent of the egg-cases parasitized) and in egg-cases from two of the small-group locations (40.7 percent and 26.7 percent parasitized). It is possibly more important that these colonies and small groups were found in the most exposed positions. In the citrus and pine plantations, trees were small (up to 5 m) and were evenly spaced at 4 to 6 m intervals. *Cyrtophora moluccensis* webs were found in nearly every tree, and as the adult webs were approximately 1/2 m in diameter, they would be a conspicuous and easily located target for parasite attacks. Webs found in the 35-year-old araucaria plantation were rarer, less evenly dispersed and not as noticeable among trees that attained 10 to 15 m. The situation in larger colonies is less clear. All large colonies are conspicuous, but the younger colonies were found in lower vegetation and were, therefore, somewhat less visible.

Although the information is scanty, one may postulate that parasite attacks (especially dipteran parasites) are most abundant in older colonies, and in colonies or smaller aggregations found in exposed locations. Inter-colony distances may be an important factor: young colonies established at some distance from the parent colony may be free from parasite attacks for a certain period of time.

Table 25. Frequency of occurrence of parasites in *C. moluccensis* egg-cases, expressed as percent of total number of egg-cases examined.

Sample No.	No. Egg-Cases Observed	% Parasitized Flies	Wasps	Both	Other	Total	Group Size	Colony Location
1	27	22.2	14.8	—	3.7[1]	40.7	≤ 5	Citrus plantation.
2	15	13.3	—	6.7	6.7[2]	26.7	≤ 5	Young pine plantation (5 yrs.)
3	23	--	4.35	--	4.35[1]	8.7	≤ 5	35 yr. araucaria plantation.
4	13	15.4	--	7.7	7.7	30.8	old colony	Telephone wires.
5	13	15.4	--	—	--	15.4	young colony	Edge of coffee plantation.
6	15	20.0	--	—	—	20.0	young colony	Tall grass.
7	10	10.0	—	—	--	10.0	young colony	Tall grass and shrubs.
8	23	4.35	—	--	4.35[1]	8.7	young colony	Tall grass and shrubs.

[1] dried eggs (cause unknown)

[2] theridiid inquiline feeding on young in egg-cases

There are no data on the frequency of occurrence of egg-case parasites in solitary orb-weaver populations (mainly because egg-cases are camouflaged and difficult to locate). A survey of 76 egg-cases of *C. monulfi* from two populations revealed only 2.8 percent and 2.4 percent parasitized or dried egg-cases. Out of 65 egg-cases of *C. cicatrosa* (one population), 6.2 percent were parasitized.

Parasitism of 30 to 40 percent of the egg-cases is a relatively high figure, and a similar incidence of parasitism would probably not be found in solitary species or in orb-weavers with well concealed egg-cases. Many questions remain unanswered. Are the hymenopteran and dipteran parasites of *C. moluccensis* host-specific? The search behavior of the dipteran parasite suggests specialization on *C. moluccensis* colonies. Are colony-dwelling *C. moluccensis* more effective in trapping dipteran parasites? Does web-shaking by one female alert nearby females to the presence of the parasites? Observations of parasite visits suggest that this may be the case: when one female began web-shaking in response to a dipteran parasite, other neighboring adult females, both with and without egg-cases, also began web-shaking. It is unclear, however, whether this was induced by the parasite itself or by the behavior of nearby females. If the latter is true, this would be an interesting colony adaptation to outside disturbance, equivalent to alarm pheromones in many social insects and warning signals in social vertebrates.

Advantages

The advantages of communal organization in *Cyrtophora* are less apparent than the disadvantages attributed to increased colony conspicsuccess and density. Some possible advantages are:

1. Increased protection of egg-cases and young.
2. Greater web building efficiency.
3. Greater prey capture efficiency.
4. Ability to exploit food resources and/or habitats that are not available to single individuals.

Data supporting these hypotheses are incomplete, and in no case is there satisfactory proof of an advantage over the solitary distribution of individuals. However, some indirect evidence is available and the implications of possible advantages of colony formation in *Cyrtophora* are worth discussing.

Protection of egg-cases and young

In the course of examining *Cyrtophora* egg-cases for parasites, two different patterns of egg-case production were distinguished (Table 26). In *C. moluccensis* and *C. annulfi* (I) only the most recent egg-case contained eggs; other egg-cases belonging to the same female invariably contained spiderlings nearing emergence or else were empty (as in most orb-weavers, spiderlings remain in the egg-case until after their first molt). *Cyrtophora cicatrosa* females (II), on the contrary, had several egg-cases each containing developing eggs. The situation in *C. cylindroides* remains unknown.

This discovery fitted neatly into the growing list of phenomena pointing toward increased parental care of offspring in the more gregarious species of *Cyrtophora*. All known species of *Cyrtophora* hang their egg-cases above the hub, in the center of the web. However, only *C. moluccensis* (and *C. citricola* in Africa, Kullmann, 1958 and

Table 26. Percentages of females of *C. moluccensis*, *C. manulfi* and *C. cicatrosa* with 1 to 6 egg-cases containing developing eggs.
n = no. of females examined

No. of Egg-Cases	I *C. moluccensis*	 *C. manulfi*	II *C. cicatrosa*
	n = 59	n = 31	n = 8
1	100	100	—
2	—	—	37.5
3	—	—	25.0
4	—	—	—
5	—	—	25.0
6	—	—	12.5

personal observations) rests under the most recent egg-case in such a way that the body and legs III and IV are in close contact with the egg-case (Chapter 3). This position is maintained throughout the day (note that dipteran parasites are diurnal), except when body temperature regulation necessitates hanging from the hub. *Cyrtophora moluccensis* females also engage periodically in tapping and "feeling" the egg-case with the legs and palps. This was observed both during the day and at night. Egg-cases that were damaged or parasitized were generally cut out and moved away from the hub or dropped entirely out of the web. There is little doubt that females can distinguish parasitized egg-cases, though the physiological basis for this remains unknown.

The somewhat gregarious *C. monulfi* females suspend their egg-cases from the walls of the retreat, the newest egg-case being the one closest to the retreat. Thus, *C. monulfi* egg-cases may be more protected than those of the solitary species, *C. cylindroides* and *C. cicatrosa*. These latter always rest under the hub and were never observed to assume a position under the egg-case. The behavior of regularly touching and palpating the egg-cases was not observed in any of these three species.

I have already mentioned that webs of immatures and juveniles were tolerated within the framework of adult webs in *C. moluccensis* colonies. This does not seem to be true of *C. monulfi* or *C. cicatrosa*. The location of immature *C. moluccensis* within the colony may ensure greater protection from predators (e.g., birds, wasps). Oddly enough, in the communal araneid, *Metabus gravidus*, immatures built their webs on the outskirts of the adult colony and moved into the main body of the colony as they grew older (R. Buskirk, personal communication). Active protection of young, or cooperation in prey capture or feeding were not observed in any species of *Cyrtophora*.

A summary of the varying degrees of protection of egg-cases and young in *Cyrtophora* is given in Table 27. The pattern of egg-case production, the active defense of egg-cases and an increased tolerance of immatures all suggest that the communal *C. moluccensis* (and probably *C. citricola*) benefits from increased protection of offspring.

Web-building efficiency

During nightly web repairs spiders were seen adding threads not only to their own webs, but to supporting structures on the periphery of the colony as well. The significance of this behavior in terms of increased web-building efficiency for the individual was not evaluated quantitatively. I can only postulate that part of the advantage must lie in the ability of each colony member to utilize the barrier web threads of its neighbors in constructing its own web. A reduction in the energy expenditure per individual in web repair and renewal is hypothesized for communal *Cyrtophora*.

Efficiency of prey capture

Numerous webs interconnected in a 3-dimensional structure should act more effectively than a solitary web in preventing the escape of flying insects. As observed time and again in *C. moluccensis* colonies, insects succeeded in escaping from one web, only to become ensnared in a neighboring one. Nevertheless, the proportion of flying insects of all groups that succeed in escaping from *C. moluccensis* colonies was very high (Table 28).

Table 27. Summary of egg-case production, defenses and care of young in four species of *Cyrtophora*. (Data on *C. citricola* are from Kullman (1958) and from casual observations of webs in West Africa and Madagascar.)

	C. moluccensis	*C. monulfi*	*C. cylindroides*	*C. cicatrosa*	*C. citricola*
I. Egg-case production					
1. egg-case produced only when previous one contains spiderlings	yes	yes	?	no	?
II. Protection of egg-case					
1. egg-case suspended in web	yes	yes	yes	yes	yes
2. female rests under egg-case	yes	yes[1]	no	no	yes
3. female periodically touches egg-case with legs and palps	yes	no?	no?	no?	yes
4. female actively protects egg-case from parasites	yes	?	no?	no?	?
III. Protection of young					
1. limited dispersal of young	yes	sometimes	no	no	yes
2. immature webs tolerated in framework of adult web	yes	no	no?	no	yes
3. female actively protects young	no	no	no	no	no?

---

[1] Egg-case attached to retreat

Table 28. Insect escapes from two *C. moluccensis* colonies. Row 1 is the total number of flying insects striking the colony (= total no. flying insects—no. avoidances). Row 2 is the percentage of insects of each order that escaped.

		Lepidoptera	Hymenoptera	Diptera	Coleoptera	Other	Unidentified	Total
Colony 1 45 hours	No. Observed	67	48	65	11	4	343	538
	% Escaped	80.6	54.2	78.5	81.8	50.0	54.5	61.2
Colony 3 40 hours	No. Observed	215	41	76	20	18	197	567
	% Escaped	93.0	95.1	94.1	80.0	72.7	65.5	82.7

As shown in Chapter 2 the non-sticky, knockdown web of *Cyrtophora* is a less efficient trap for flying insects than the typical sticky orb-web. By experimentally flying blowflies into solitary webs of *C. moluccensis*, it was shown that the knockdown web was less effective both in initially trapping flying insects and in restraining them once they were trapped. Thus, the large number of escapes observed in *C. moluccensis* colonies may be partly explained by the relative inefficiency of the individual web. Robinson and Robinson (1970) recorded by indirect methods approximately 5 percent escapes from solitary *Argiope argentata* webs, recently R. Buskirk (personal communication) observed 45 to 50 percent escapes from colonies of *Metabus gravidus*, a figure more comparable to those obtained from *C. moluccensis* colonies. The discrepancy between the *Argiope* figures, on the one hand, and the *Metabus* and *Cyrtophora* figures on the other may be due in part to the different recording techniques. However, the possibility also exists that communal species, by virtue of their ability to occupy habitats with a super-abundance of prey, can "afford" to lose more prey. This is discussed later. So far, there is no concrete evidence that colony members have greater prey capture success than solitary *C. moluccensis*.

Habitat exploitation

Cyrtophora moluccensis colonies are generally located in open spaces and may bisect major flight paths of insects. These habitats may be favored locations because of an abundance of potential prey, but they are generally unavailable to solitary web-building spiders. The colonies benefit in particular from the abundance of nocturnal insects, especially moths, which utilize the gaps between trees as flight paths. Although diurnal Lepidoptera successfully avoided colonies, nocturnal moths constituted approximately 30 to 45 percent of the total prey (by number) of C. moluccensis individuals in three colonies over a period of one year (Lubin, in preparation). Furthermore, C. moluccensis captured more prey at night, when the colony was virtually invisible, than during the day, for at least part of the study period. It is possible, however, that some night-flying insects can avoid colonies by the use of sonar [noctuid and arctiid moths are known to emit ultrasonic "clicks" (Roeder, 1967) much in the manner of bats].

A rough estimate of the abundance of potential prey in the vicinity of two C. moluccensis colonies was calculated from data on flying insects obtained during 85 hours of day and night observation. All insects striking the colonies or actively avoiding them were recorded. An average of 775/45 = 17.2 insects per hour were observed flying toward colony 1, or approximately 413 insects per 24 hours. Likewise 1033/40 = 23.3 insects flew toward colony 3, or approximately 559 insects per 24 hours. During the period of observation there were approximately 75 individuals (of all ages) in colony 1 and 30 individuals in colony 3. Thus, the number of prey potentially available would be 5.5 insects per individual per 24 hours in colony 1 and 18.8 insects in colony 3. As approximately 20 percent of the individuals in colony 1 and 30 percent in colony 3 were immatures with lower food requirements, proportionally more insects would be available to adult members of the colony. The difference between the two colonies may be due partly to seasonal effects, as colony 1 was observed during the beginning of the "dry" season and colony 3 during the "wet" season. As shown elsewhere, however, large scale seasonal variations in rainfall and insect abundances were not encountered in Wau (Lubin, in preparation).

Compare these figures with data on *Argiope argentata*, an inhabitant of grass and low vegetation in Panama (Robinson and Robinson, 1970): an average of 1.6 insects struck an individual web per web-day (4672 prey captures and escapes in 2809 web-days). A web-day in *A. argentata* is approximately 10 hours; *A. argentata* is active in prey capture only during the day, while *C. moluccensis* can be active throughout 24 hours. As there is no record of the number of insects avoiding *A. argentata* webs, and probably not all insect escapes were recorded, this figure is an underestimate. But even assuming 50 percent web avoidance (i.e., 50 percent of all insects approaching an *Argiope* web succeed in avoiding it), the doubled figure of 3.2 insects per web per web-day falls short of the estimate of flying insects available to *C. moluccensis*. As *C. moluccensis* and *A. argentata* adults are approximately the same size and weight and have webs of similar diameter, I think the above comparison is valid.

Thus, perhaps *C. moluccensis* compensates for its relatively inefficient web by extending its predatory activity period and by exploiting habitats in which there is an abundance of available prey and few araneid competitors. It is worth noting that as soon as a *C. moluccensis* colony becomes established, other araneid species begin to build on the periphery, using the communal webs as supports. Especially common are webs of *Nephila maculata* and *Leucauge* sp., both of which form occasional loose aggregations by themselves (much like those of *C. monulfi*).

Assuming that the non-sticky, knockdown web of *Cyrtophora* allowed spiders of this genus to expand into exposed, previously unexploited habitats (Chapter 2) why have only *C. moluccensis* and *C. citricola* evolved communal organization, and why has *C. cylindroides* reverted to occupy denser, forest habitats? A size factor is likely to be important in the evolution of communal organization: the smaller species (e.g., *C. monulfi*, *C. cicatrosa*, and sp. "D") may be small enough to obtain sufficient food in open, grassland areas, where they are found alongside other araneids such as *Cyclosa*, *Argiope* and *Araneus* spp. Colony formation in *Cyrtophora* is conceived as one solution to the problem of obtaining sufficient prey in a larger species. *Cyrtophora cylindroides* may achieve the same goal without communal organization by utilizing rare and possibly more stable microhabitats.

Population Dynamics

Colony Formation

Two natural colonies and one experimental colony were observed in the early stages of growth. The growth of colonies 1a and 2 is shown in Figures 12 and 13. Both incipient colonies were located near colony 1, a large colony approximately one year old; 1a was on the opposite side of the same pine tree and 2 was across a path, approximately 3 m from 1a. As colony 1 was the only one in the immediate vicinity, it was most likely the parent colony of 2, colony 1a was definitely formed as a result of dispersal of immatures from colony 1. From the beginning of the study period in May 1970, immature *C.*

Figure 12. Weekly census of numbers of immatures (< 10 mm), subadults and adults without egg-cases, and adults with egg-cases in colony 1a.

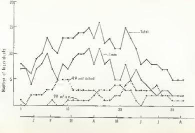
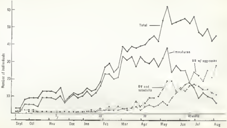

Number of Individuals
20
15
10
5
Total
Imm
♀♀ and subad
♀♀ w/ y.c.
1
10
20
30
J
F
M
A
M
J
J
A

Figure 13. Weekly census of numbers of immatures (< 10 mm), subadults and adults without egg-cases, and adults with egg-cases in colony 2.


Number of individuals
60
50
40
30
20
10
Total
Immatures
♀♀ w/ egg-cases
♂♂ and subadults
1
10
20
30
40 weeks
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug

moluccensis were observed periodically in the location of colony 1a. However, the first sub-adults did not appear until December, 6 months later, and the first egg-cases appeared early in February of 1971. Colony 1a remained unsuccessful and was declining in numbers at the end of the study period. Colony growth is initially slow, as can also be seen in colony 2. First records of colony 2 in September of 1970, were of 2 adults (one with an egg-case) and one immature. The colony growth rate was low for 4 1/2 months, until mid-January of 1971, when it increased sharply I will return to the essentially sigmoid nature of the colony growth curve later.

It is unclear whether colony 2 was established initially by immatures, or by adults or subadults. Observations on web renewal frequency indicated that an adult will not move out of a colony unless its web has been destroyed or the web-site made unattractive, either due to habitat destruction or occupation by another adult. Adults will build new webs in new locations, however, as seen clearly when adults were released near the house. Furthermore, the adults tended to clump and build their webs near each other, rather than disperse in the surrounding vegetation. Three separate releases of 4 to 10 adults each resulted in 3 new colonies (one near a mercury-vapor lamp on the porch, the second in the electricity and telephone wires above the house, and the third under the eaves of another house).

As web destruction and habitat destruction are not frequent occurrences, it is likely that most new colonies are initiated by dispersing young. Newly hatched *C. moluccensis* remain near the egg-case for 3 to 6 days after hatching, spinning a protective(?) matrix of silk around themselves; after that period they begin to disperse and build individual webs (Table 29). The young tend to disperse upward in the colony, building their webs within the barrier webs of the adults. Some young also move away from the colony into surrounding vegetation, however, dispersal by means of ballooning, a common phenomenon in many araneids, was not observed in *C. moluccensis*. Although dispersal was not studied in detail, there is some indication that immatures tend to clump in young, incipient colonies, but disperse from older colonies.

Kullmann's (1984) observations on dispersal and colony formation in *C. citricola* indicate a pattern similar to that of *C. moluccensis*. He released two egg-cases in the garden of the Institute of Parasitology in Bonn, Germany (at least 8° latitude above the northern limit of this species). The young hatched after approximately three weeks incubation and remained near the egg-case for 8 to 10 days, at this time the young began to disperse and build webs. Ballooning was not observed in *C. citricola*. In the laboratory, Kullmann noticed that immatures were attracted to light, a behavior which would account for the tendency of young to move upward in the colony. Eleven weeks after hatching 57.8 percent of the immatures had built webs within a 10 m radius of the egg-cases, no webs were found further than 80 m from the point of origin.

Thus, dispersal in *C. citricola*, as in *C. moluccensis*, appears to be limited in range, even in the immature stages. Such limited dispersal of young is, indeed, an unusual phenomenon in an order renowned for its aeronauts. Gertsch (1949) cites records of ballooning spiders more than 200 miles from the nearest land and Gressitt (1961) found a large number of spiders in aerial traps in the Pacific, 360 miles from the nearest probable point of origin. However, it is possible that dispersal by ballooning, so spectacular an occurrence in temperate spiders, does not occur as often in tropical species. There may be some similarity between mechanisms of plant seed dispersal and of spiderlings, with a reduction in the number of wind-borne elements in forest understory (and forest-clearing?) species as seen in rainforest plants (Richards, 1966). Dispersal of tropical orb-web spiders has not been studied and the subject warrants further attention.

Colony Growth

The growth curves of colonies 2, 1, and 3 (Figures 13, 14, and 15) may represent, respectively, 1) formation and early growth, 2) stabilization, and 3) equilibrium stages of colony development. As mentioned above, the early colony growth curve appears to be sigmoid in shape, thus following a pattern typical of non-communal animal populations. Looking at growth rates of immatures, adults and subadults and adults with egg-sacs separately, one can see that initial colony growth was due to a rapid increase in the number of immatures. There was then a 3 to 6 month lag before the number of adults began to climb, which is slightly longer than the duration of development to maturity as recorded in an experimental colony (approximately 4 months, Table 29) As the experimental colony was situated near a mercury-vapor lamp for attracting insects and had an excess of food, individual development rates may have been accelerated. Turnbull (1962, 1965) found that increased food supply accelerated the

Figure 14. Weekly census of numbers of immatures (< 10 mm), subadults and adults without egg-cases, and adults with egg-cases in colony 1

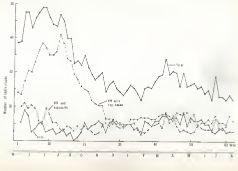

Number of individuals
80
60
40
20
Total
♀♀ with egg-cases
♀♀ and subadults
Imm
1
10
20
30
40
50
60 Wks
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A

Figure 15. Weekly census of numbers of immatures (< 10 mm), subadults and adults without egg-cases, and adults with egg-cases in colony 3.

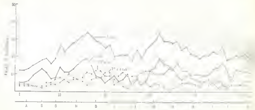

50
1
10
A
S
O
N
D

Table 29. Time intervals (in days) of development of *C. moluccensis* from egg to adult, and of production of egg-cases by adults, based on data from solitary individuals and small colonies.

	Egg-Cases Incubation Period		Immatures		Adults		
Female #	#1	#2	Emergence to Dispersal	Emergence to Adult	Copulation to Egg-case #1	Egg-case #1 to Egg-case #2	Egg-case #2 to Egg-case #3
1	27	50	3-5	120 (ca.)		11	58
2	32					27	11
3	43		7-8			50	
4						19	
5					15		
6						37	
n	4		2 groups	1 adult	1	5	2
M	38.0		3-8	120	15	28.8	34.4
S.D.	18.4					15.3	18.6

growth of the spiders *Linyphia triangularis* and *Agelenopsis potteri*, and it is probable that this relationship holds for most spiders, as it does for many other invertebrates.

An interesting phenomenon was observed in colony 1 (Figure 14), which was approximately 1 year old at the beginning of the census and in the last phase of initial growth. Instead of leveling off at approximately 70 individuals, the colony decreased in size over a 2-month period, finally attaining a more-or-less stable population size of 25 to 35 individuals. The decrease in colony size was due almost entirely to adult mortality (and emigration?). The obvious questions are: 1) what caused adult mortality and 2) why did the colony stabilize at a size approximately 1/2 the maximum colony size observed during growth? Although the answers are by no means clear, there are several points worth considering. The decrease in number of adults, which began in mid-August, came more than 4 months after the initial increase in the adult population size. The adult life span of *C. moluccensis* was calculated to be approximately 3 1/2 months (Table 30), though some adults were observed for over 5 months. Thus, the observed adult mortality in colony 1 may be partly explained in terms of the normal adult life span.

The decrease in number of individuals in colony 1 fell at the end of the dry season and the beginning of the major wet season. The phenomenon of colony growth and subsequent decrease did not, however, repeat itself in the next dry-wet seasonal cycle, colony size and age distribution remained stable throughout the remaining census period. The lack of any large-scale seasonal fluctuations in population size

Table 30 Life-span in days of adults with 1 to 6 egg-cases, estimated by taking known intervals from first observed egg-case until disappearance of adult (death) + average intervals between previous egg-cases from time of last molt. Average intervals between successive egg-cases are given in Appendix 2.

No Egg-Cases Per Adult	No Adults	Mean Life-Span ± S.D.	Range
1	3	77.5 ± 9.5	76.5 - 87.5
2	5	86.7 ± 22.4	64.5 - 119.5
3	8	117.5 ± 23.5	75.2 - 153.0
4	2	130.6 ± 5.1	127.0 - 134.2
6	1	151.2	
Total	19	106.2 ± 28.6	64.5 - 153.0

can also be seen in the older colony 3 (Figure 15). Colony size fluctuated between 20 and 30 members and the age distribution was relatively stable. The smaller fluctuations in the size of colony 3 were due mainly to non-seasonal changes in numbers of immatures. These observations suggest that after the initial colonization and period of rapid growth, colonies reach an optimal size and age distribution with regard to the available resources and maintain that level throughout the year(s) without any major changes. The ultimate reason for the fluctuation observed in colony 1 remains unknown. Two possibilities are suggested: 1) A distinct qualitative change in the habitat occurred during August to September of 1970, resulting in a reduction of the carrying capacity of the environment (lower K). 2) A combination of factors such as prey abundance and web site availability led to an "overshoot" in colony size during the phase of exponential growth, which was corrected as conditions became less favorable. The two hypotheses are not necessarily mutually exclusive. It is significant that the formation of colony 2 occurred in August of 1970, at approximately the time colony 1 began to decrease in size. Perhaps the site of colony 1 became less favorable (or saturated) and that at this stage immatures began moving away from the parent colony.

The lack of seasonality found in *C. moluccensis* colonies is, in itself, an unusual phenomenon. Robinson and Robinson (unpublished) observed dramatic fluctuations in population sizes of *Nephila maculata* in certain areas in Wau: the number of immatures increased after the beginning of the wet season and remained high until the start of the dry season (these fluctuations may be less evident in forest habitats). Numbers of *Argiope argentata* in a forest clearing in Panama were observed to fluctuate seasonally (Robinson and Robinson, 1970); Emmel and Leck (1970) observed seasonal changes in population sizes of several pierid and papilionid butterflies in the same clearing and other records of the effects of tropical wet-dry seasonal cycles on population size are cited in their bibliography. Robinson and Robinson's (1970) study of the prey of *Argiope argentata* indicates that availability of prey is at least partly responsible for the fluctuations in spider population size. Censuses of the prey of *C. moluccensis* and of the available flying insects near the colonies over a period of one year showed no consistent seasonal pattern (Lubin, in preparation). Nonetheless, since nearby populations of *N. maculata* exhibit distinct seasonality, the seasonal pattern of *C. moluccensis* colonies still remains to be explored.

Earlier I postulated that the communal *C. moluccensis* occupies a niche in which food is essentially non-limiting. It does this by 1) a temporal extension of prey capture activities, and 2) exploitation of prey-rich areas which are also poor in competing predators. The pattern of colony formation and growth also implies an aseasonal and non-limiting food supply, but instead there seem to be other limiting factors which maintain colony size at an equilibrium level. Possibilities include lack of space for colony expansion and high incidence of parasitism and predation on young (evidence for this was presented above). One must remember, however, that *C. moluccensis* is a widely distributed species, both geographically and ecologically, and inferences made from studies in one location may not apply to colonies in other locations.

In many respects, *C. moluccensis* behaves as a colonizing species. Wilson (1971) draws a comparison between incipient colonies of social insects and island propagules. Traits that may preadapt species to be good colonizers are listed by MacArthur and Wilson (1967) as 1) preference for "marginal" habitats, 2) ability to disperse, 3) large K (= carrying capacity), and 4) large r/λ or large intrinsic rate of increase (r), with a low death rate (λ). *Cyrtophora moluccensis* fulfills at least some of these requirements: it occupies "marginal" habitats, it can maintain large population sizes and is capable of rapidly increasing colony size, at least during initial stages of colony growth.

MacArthur and Wilson (1967) defined "marginal" habitats as "habitats containing relatively low species diversity," and stated that this may be due to either marginal physical conditions or other causes. Although numerous araneids occupy forest-ecotone and forest-clearing habitats in the tropics, the micro-habitat of *C. moluccensis* (and *C. citricola*) is indeed species-poor. The adaptations that enable exploitation of such exposed habitats, as shown in Chapter 2, are found in relatively few spiders, e.g., the communal theridiids and *Cyrtophora* species. Since these habitats are poorly exploited, a colonizing *C. moluccensis* "propagule," faced with unlimited resources, will probably grow exponentially (Lewontin, 1965). The data on early stages of colony growth support this. The high population density found in colonies may also enhance the colonizing success of

C. moluccensis. Successful colonies of *C. moluccensis* are often large (colonies of over 200 members were observed) and essentially immortal. Short-range dispersal in *C. moluccensis* is successful; as mentioned above, within one year, two new colonies were established by dispersal from colony 1.

There is evidence that *C. moluccensis* is also capable of long-range dispersal, in spite of the apparent lack of ballooning of young. In New Guinea, the species is found not only in inhabited coastal areas, but also in the most remote native villages in the mountainous interior [e.g., in the Telefomin and Liptimin village complexes in the Star Mountains (West Sepik District) and in the isolated Menyamya villages of the Morobe District]. *Cyrtophora moluccensis* was not (to my knowledge) found in areas undisturbed by man, and the densely forested mountain ranges may be an ecological barrier for this species. As the New Guinea villagers often transplant their ornamental shrubs and trees when a new village is established, it is likely that *C. moluccensis* egg-cases or young are accidently transported by man to each new location. Gardner and Heider (1968), in their book on the Dani tribes of the Baliem Valley in West Irian, show a photograph of a *C. moluccensis* colony, captioned:

> Spiders are collected in the forests and brought to the compounds where they weave elaborate webs. These webs are compressed into magically protective strips which hang from the throat or, more rarely, are formed into hats.

This suggests that at least some New Guinea tribes transplant *C.*

moluccensis colonies intentionally. *Cyrtophora moluccensis* has not only colonized much of New Guinea, but is widely distributed throughout the South Pacific from Southern Japan to northeastern Australia. Again, it is possible that man has played a large part in the wide distribution of this species throughout the Pacific.

Summary

Colony members in the communal orb-weavers, *C. moluccensis*, interact aggressively during prey-capture activities and during web-building and web repair. Such interactions may constitute a spacing mechanism to ensure an adequate food supply for each individual. Some disadvantages of communal organization, e.g. increased parasite loads and web avoidance by flying insects, are related to the visual conspicuousness and persistence of *C. moluccensis* colonies. Advantages of communal organization are postulated as follows:

1. Increased protection of egg-cases and offspring.
2. Greater web-building efficiency.
3. Greater prey capture efficiency.
4. Utilization of "marginal" web-sites that are poor in other araneid species, but rich in available food.

Evidence is presented supporting the first and last of these hypotheses.

Increased body size and greater energy requirements may have promoted the evolution of communal organization in *C. moluccensis* and *C. citricola*. An alternative solution of increased rarity (and specialization?) is postulated for *C. cylindroides*. Hopefully, the questions raised in this discussion will stimulate further research on the adaptive value and evolution of sociality in spiders.

Population dynamics of *C. moluccensis* colonies in three different growth phases are described. In favorable sites, initial colony growth was rapid, stabilization occurred at a population size that was lower than the maximum size during the period of rapid growth. The size and age distribution of the colonies studied did not fluctuate seasonally. *Cyrtophora moluccensis* appears to fit the pattern of a colonizing species. Although this may be true of many forest-clearing species of orb-web spiders, *C. moluccensis* may be more successful due to its rapid growth rate, high population density, ability to exploit marginal and disturbed habitats and, possibly, greater potential for dispersal.

APPENDIX 1. METABOLIC RATE MEASUREMENTS

Average metabolic rates of adult *C. moluccensis* from Wau, New Guinea were determined by oxygen consumption measurements at 30°C. Spiders were acclimated at 30°C and natural light conditions for 2 to 3 days prior to measurement. During this period they were not fed, nor were they allowed to build webs. Acclimation periods of 2 to 3 days were found by Anderson (1970) to be sufficient for a variety of spiders. Although 30°C is probably somewhat higher than the average temperature in Wau, temperatures of 29°C to 31°C were recorded daily in the shade. Since *C. moluccensis* occurs in exposed, sunlit areas, it undoubtedly faces daily temperatures exceeding 30°C.

Oxygen consumption was measured using a Warburg apparatus. Measurements were made in 65 ml flasks, with a piece of filter paper soaked with 2 ml of a 50 percent KOH solution to absorb CO_2 placed in the bottom and separated from the spider by a wire screen. Oxygen consumption measurements were corrected to µl O_2 consumed at 0°C and 760 mm Hg (STP).

Oxygen consumption in *N. clavipes* was measured using a Gilson Differential Respirometer. All measurements were made at 25°C on spiders which had been acclimated at this temperature for 2 to 5 days. 125 ml flasks were used, with a layer of soda-lime (Sodasorb, high moisture) to absorb CO_2. Techniques used are similar to those described by Anderson (1970).

Oxygen consumption measurements, corrected to STP, were converted to calories by taking 1 µl O_2 = .0048 calories (Engelmann, 1961).

APPENDIX 2. AVERAGE INTERVALS IN DAYS BETWEEN SUCCESSIVE EGG-CASES OF *C. MOLUCCENSIS* ADULTS, DERIVED FROM FIELD OBSERVATIONS ON SMALL COLONIES.

Period	n	Mean ± S.D.	Range
Last molt to Egg-case #1	2	34.5 ± 7.5	27-42
Egg-case #1 to Egg-case #2	15	24.7 ± 9.8	10-36
Egg-case #2 to Egg-case #3	6	32.8 ± 14.7	16-56
Egg-case #3 to Egg-case #4	4	30.2 ± 9.3	17-40
Egg-case #4 to Egg-case #5	1	13	
Egg-case #5 to Egg-case #6	1	13	
Total	29	27.0 ± 11.8	10-56

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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